THE OSTEOLOGY AND MYOLOGY OF THE CRANIOCERVICAL REGION IN SQUAMATE REPTILES: A COMPARATIVE STUDY

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"There is not a moving (living) creature on earth nor a bird that flies with its two wings, but are communities like you. We have neglected nothing in the Book, then unto their lord they all shall be gathered"

Holy Qur'an 6:38

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ABSTRACT

Modern squamates (lizards, snakes and amphisbaenians) form a highly successful group of terrestrial reptiles with a range of habitats and lifestyles. Some features of their anatomy (head, limbs) are relatively well-studied, but there are significant gaps in our knowledge. The neck is one such area. It provides the mobile unit between the head and the body, serving for the attachment of the musculature to the head, the forelimb and the pharyngeal region. The mobility of the head is dependent on arrangement of such muscles and on the structure of the craniovertebral and intervertebral joints across which the muscles act. Preliminary studies have shown interesting patterns of variation in both skeletal anatomy and musculature. The aim of the project was to explore, catalogue and analyse this variation, and to find functional and/or taxonomic explanations for it. Details of the surface morphology of bones, and the origin and insertion of muscles were recorded for *Caiman*, *Sphenodon* and squamates (including the amphisbaenian *Diplometopon* and the snake *Trimeresurus*). Where possible, comparisons were also made within and between taxa to determine levels of inter- and intraspecific variation, as well as variation between genera. Several limbless or limb-reduced taxa were compared to assess levels of convergence in these forms. The results of the study suggest that some craniocervical characters may be phylogenetically useful although there is a high level of variation within and between species. Craniocervical characters generally support the monophyly of Lepidosauria, Squamata

and Scleroglossa (all non-iguanian squamates); and major clades like Iguania, Gekkota, Scincomorpha and Anguimorpha. Also supported are groups like Acrodonta (agamids + chamaeleons) and Scincoidea; and families like Chamaeleonidae and Varanidae. Within Squamata, craniocervical features seem to place Gekkota closer to Anguimorpha than Scincomorpha. Varanid lizards and snakes (*Trimeresurus*) share muscular features (origin and extension of longus colli in the craniocervical region), although varanids themselves are distinctive in their neck morphology. Amongst the limbless taxa examined, the amphisbaenian *Diplometopon* and the snake *Trimeresurus* had a specialised neck morphology which differs from that of lizards, but the craniocervical features of *Diplometopon* resembled those of gekkotans and limbed anguimorphs (e.g. varanids) more than scincomorphs.

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Figures = Hand drawings under Wild stereomicroscope, fitted with camera lucida.
Plates = A number of figures.

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I - INTRODUCTION

CHAPTER (1)

1.A) Section

General introduction

.... Why a neck? ... The vertebrate head contains a concentration of major sense organs and neural control centres, as well as the openings into the respiratory and digestive systems. The amniote neck connects the head to the trunk facilitating its movement in food acquisition (reaching stationary or mobile food items), defence (e.g. biting or butting predators), and the monitoring of the environment for visual, auditory and chemosensory cues. The skull of an agnathan fish articulates directly with the notochord, but in jawed fish, the skull is very closely associated with the bony vertebrae at their first appearance (Gans, 1992a). In fish, the vertebrae are not differentiated into functional regions (except in the tail), and the pectoral girdle is attached directly to the skull. The very earliest tetrapods, such as the Devonian *Acanthostega* (Coates, 1996), show a similar condition. As a result, the girdle cannot move independently of the head, a severe limitation for a terrestrial animal. Effective terrestrial locomotion required a number of key changes – consolidation of the vertebrae (fusion of components of the arch and centrum), the freeing of the girdle from the skull, the development of an effective craniocervical joint, elongation of the vertebral column between the head and trunk, and the regionalisation of the vertebrae into functional groups (Romer, 1956). Some of these changes are seen in amphibians, including the specialisation of the first

vertebra (atlas) permitting improved flexion and extension of the head (e.g. Jouffroy, 1992). An atlantooccipital joint was also present in the ancestors of amniotes (Romer, 1956), but further changes within early amniotes facilitated the occupation of the terrestrial environment. These included the development of a specialised rotatory joint between the atlas and the second vertebra (axis), giving increased craniocervical mobility, in conjunction with a lengthening and strengthening of the cervical region. The result was a fully functional and mobile neck (Romer, 1956; Gans, 1992a). Once the fully terrestrial amniote condition had developed, there was a fairly rapid diversification of land animals into different feeding and locomotor niches. As part of this radiation, including the move back into the aquatic environment and the conquest of the air, the neck played an important role during orientation of the head, and in feeding in mammals (Bekele, 1983), birds (Zweers, 1982), crocodiles (Cleuren and De Vree, 2000), and lizards (Smith, 1982). Strong necks with massive neural spines evolved to support the heavy heads of large herbivores (e.g. elephants, ceratopian dinosaurs) and powerful predators (e.g. carnosaurian dinosaurs); greatly elongated necks aided food acquisition in water (e.g. plesiosaurs [*Muraenosaurus* = 76 cervical vertebrae – Young, 1981], nothosaurs, tanystropheids, some aquatic turtles, e.g. Pritchard, 1984) and on land (sauropod dinosaurs, giraffes); and flexible necks could be used for bending (Bellairs, 1969), or to draw the head into protective cover (e.g. chelonians). The posterior cervical vertebrae of the chelid *Hydromedusa* have strong lateral processes, where strike forces are generated by the elongated neck during predation (Pritchard, 1984). Such an elongation

also permits the trunk to remain underwater with the head extended for breathing and a much more efficient monitoring of the environment. Some birds (e.g. the noisy scrub-bird – Zusi, 1985) use their bill rather than feet for clearing the ground in searching for food by poking their head under the litter. This could involve the hypertrophy of their neck muscles (Smith, 1976; Zusi, 1985). This increasing specialisation of the neck in amniotes is reflected not only in the increasing complexity of the bones and their joints, but also in the differentiation and elaboration of the craniocervical musculature, the main subject of this thesis.

1.A:1) The history and phylogeny of Lepidosauria

On the basis of skull structure, amniotes have long been divided into four major lineages: anapsids (no temporal skull openings, e.g. chelonians); parapsids or euryapsids (a single upper opening, e.g. plesiosaurs); synapsids (a single lower opening, e.g. mammals and all their fossil relatives); and diapsids (upper and lower openings, e.g. birds, crocodiles and lizards) (e.g. Romer, 1956; Young, 1981; Benton, 1982, 1985; King, 1996). Today, Diapsida is a formally recognised group including a number of extinct fossil lineages and two major clades – Archosauromorpha (e.g. birds, dinosaurs, crocodiles – Benton and Clark, 1988) and Lepidosauromorpha (e.g. Evans, 1988; Gauthier et al., 1988). The earliest recorded diapsid is currently the genus *Petrolacosaurus* (Reisz, 1981) from the Carboniferous of the USA. Lepidosauromorpha (Gauthier et al., 1988) comprises Lepidosauria and a few stem taxa related to lepidosaurs (e.g. kuehneosaurs, *Marmoretta*; Evans, 1988, 1991). Lepidosauria itself includes Rhynchocephalia (the living New Zealand Tuatara *Sphenodon* and its fossil

relatives), Squamata (lizards, snakes and amphisbaenians) and all descendants of their last common ancestor (Peters, 1982; Evans, 1984, 1991; Benton, 1985; Estes et al., 1988; Gauthier et al., 1988; Rieppel, 1988). Rhynchocephalians are known from the beginning of the late Triassic (Fraser and Benton, 1989) and have a relatively good fossil record until the mid-Cretaceous when they disappeared from northern continents. Squamates are the most successful group of living reptiles numbering more than 6,000 species. They have a highly distinctive morphology and the group, as currently recognised (e.g. Estes et al., 1988; Evans, 1988; Gauthier et al., 1988; Rieppel, 1988), is certainly monophyletic. Squamates probably evolved during the Triassic but are not recorded in the fossil record until the Middle Jurassic (Evans, 1994, 1998). Estes et al. (1988) divided squamates into Iguania and Scleroglossa. Iguania are recorded from the Late-Cretaceous (Estes, 1983), although new fossils from India suggested they were present in the early-mid Jurassic (Evans et al., 2000). Romer (1956) and Estes et al. (1988) divided Iguania into three families: Iguanidae*, Agamidae* and Chamaeleonidae. Agamidae* and Chamaeleonidae form the Acrodonta (Estes et al. 1988) which is closely related to Iguanidae* (Camp, 1923; Moody, 1980; Rieppel, 1988). According to Estes et al. (1988) and Frost and Etheridge (1989), Iguanidae* and Agamidae* may not be monophyletic groups (metataxa) and they proposed a division of subfamilies (e.g. Iguanidae* is divided into 8 subfamilies: Hoplocercidae, Polychrotidae, Corytophanidae, Phrynosomatidae, Crotaphytidae, Iguanidae, Opluridae and Tropiduridae).

Scleroglossa encompasses snakes (Serpentes), amphisbaenians (e.g. the burrowing *Amphisbaenia*), the poorly know limbless Dibamidae, and three major groups of lizards – Gekkota, Scincomorpha and Anguimorpha (Estes et al., 1988). Scincomorphs and anguimorphs are known from the Middle Jurassic (Evans, 1998), while gekkotans are recorded from the early Cretaceous (Alifanov, 1993). Some studies place Gekkota close to Scincomorpha (Presch, 1988), or Gekkota close to Anguimorpha (Evans and Chure, 1998; Gao and Norell, 1998; Reynoso, 1998); others unite Anguimorpha and Scincomorpha (Camp, 1923).

Of these major groups, Gekkota, which includes Eublepharidae, Gekkonidae and Pygopodidae, is well supported by McDowell and Bogert (1954), Underwood (1957), Kluge (1967), Estes (1983), and Estes et al., (1988). Scincomorpha contains the families: Scincidae, Cordylidae, Lacertidae, Teiidae, Gymnophthalmidae, and possibly Xantusiidae (Camp, 1923; Savage, 1963; Rieppel, 1976; Estes, 1983; Arnold, 1984; Estes et al., 1988). A relationship between lacertids, teiids and gymnophthalmids is widely supported (Camp, 1923; Estes, 1983; Estes et al., 1988; Rieppel, 1988; Hallerman, 1998), while scincids and cordylids are also frequently linked (e.g. Camp, 1923; Estes, 1983; Gauthier, 1984; Estes et al., 1988; Rieppel, 1988; Evans and Chure, 1998; Hallerman, 1998). Lee (1998), however, united scincids and cordylids with anguimorphs to form a group, Diploglossa. The relationships of xantusiids are not clear.

Most authors consider Anguimorpha to be monophyletic (Estes et al., 1988; Evans and Barbadillo, 1997; Lee, 1997). Living anguimorphs include anguids, xenosaurs and varanoids (varanids, lanthanotids and

helodermatids – Rieppel, 1980; Gauthier, 1982; Pregill et al., 1986; Estes et al., 1988), although, again the relationships of these three are not clear (e.g. Evans and Barbadillo, 1997; Gao and Norell, 1998; Lee, 1998). Varanoid relatives are known from the Middle Jurassic onwards (Evans, 1994), but in the Cretaceous, several specialised aquatic lineages appeared; including the elongated dolichosaurs; the aigialosaurs; and the large mosasaurs (Russell, 1967; Lee, 1997).

Haas (1980) suggested that dolichosaurs were the ancestors of snakes, but Caldwell and Lee (1997), Lee (1997, 1998), Lee and Caldwell (1998), and Lee et al., (1999) have argued that the marine mosasaurs were snake ancestors. This view has been strongly disputed by Rieppel and Zaher (2000) and by Tchernov et al., (2000), who placed living Monitor lizards (varanids) closer to Amphisbaenia and snakes.

Snakes are first known from the Early Cretaceous (Gardner and Cifelli, 1999), and form a large and very successful group composed of the small burrowing Scolecophidia (Typhlopidae, Leptotyphlopidae and Anomalepididae) and the advanced and more diverse Alethinophidia which consists of burrowing (e.g. Uropeltidae) and non-burrowing (e.g. Viperidae) types (Webb, et al., 1978; Halliday and Adler, 1986; Shine, 1992; Zug, 1993). Many authors have been impressed by the similarities between snakes and varanoid lizards (Camp, 1923; McDowell and Bogert, 1954; McDowell, 1972; Bellairs, 1972; Lee, 1997).

Amphisbaenian relatives are first recorded from deposits of late Cretaceous age (Wu et al, 1993, 1996), but their relationships with other scleroglossans are not resolved. Some studies support the relationship

between amphisbaenians and dibamids (Greer, 1985; Rieppel, 1984, 1988), while others connect amphisbaenians and teiids (Wu et al., 1993, 1996; Schwenk, 1988). Underwood (1957), Caldwell (1998), Lee (1998) and Reynoso (1998) linked amphisbaenians with gekkotans, but other authors support a relationship between amphisbaenians, dibamids and snakes (Hallerman, 1998; Rieppel and Zaher, 2000; Tchernov et al., 2000). Convergence is a major problem in resolving the relationships of limbless and limb reduced forms. The elongated limbless body form seen in living snakes and most amphisbaenians has evolved repeatedly in many families of scleroglossan lizards, and this can make it difficult to separate phylogenetic similarity from convergence due to lifestyle.

The following tree represents a summary of the lepidosaurian phylogeny agreed by most authors. This consensus tree also forms the basis for later discussion of craniocervical characters.

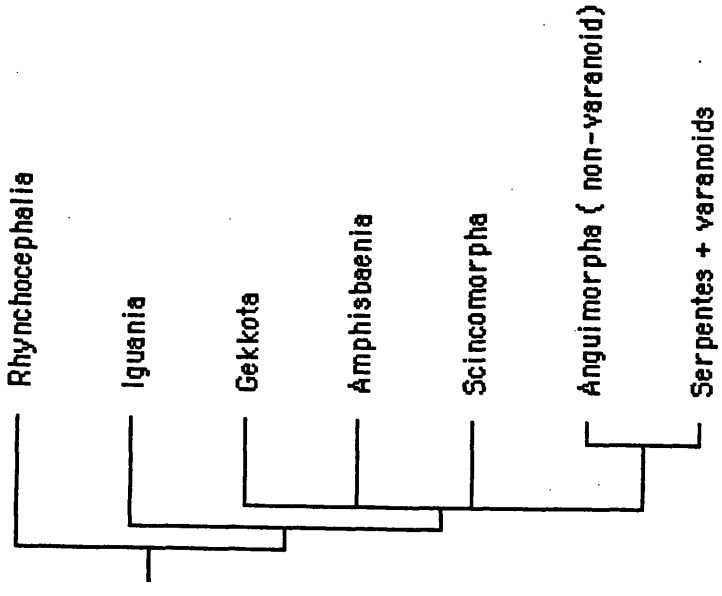


Diagram (1.A:1) basic consensus tree of lepidosaurian phylogeny agreed by most authors.

1.A:2) The evolution and diversification of the neck in Lepidosauria

A majority of living lepidosaurs have seven or eight cervical vertebrae and this was probably the primitive condition. The most primitive known lepidosaur is currently the early Jurassic rhynchocephalian *Gephyrosaurus* (Evans, 1980, 1981). Although the cervical count is not known, the genus had short gracile cervical vertebrae, with relatively simple intervertebral joints (zygapophyses, very rudimentary zygosphenes and zygantra), persistent simple intercentra between vertebrae, and notochordal amphicoelous vertebral centra. This is closely similar to the condition in the living *Sphenodon*. Like *Sphenodon*, *Gephyrosaurus* appears to have lacked ribs on both the first and second cervical vertebrae, with the first unicapitate cervical ribs (at least in the adult) on vertebra three. The living *Sphenodon* has a proatlas element between the atlas and the back of the skull, and this was probably the case in *Gephyrosaurus*.

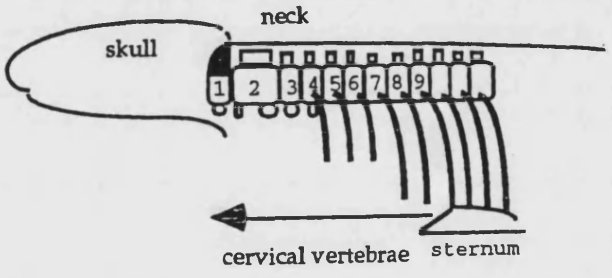


Diagram (1.A:2) Computer diagram showing left lateral view of a primitive cervical vertebral count of 8 vertebrae in the anguid *Elgaria multicarinata*.

Within Rhynchocephalia, this cervical morphology was retained relatively unchanged. In Squamata, there has been a greater degree of diversification, principally with respect to vertebral number and neck length; the structure of the intervertebral joints; the pattern of the intercentra; and the pattern and arrangement of the cervical ribs.

Most living squamates retain the primitive cervical vertebral count, with a minimum of five vertebrae in chamaeleons and a maximum of nine in varanids (Hoffstetter and Gasc, 1969; Rieppel, 1980). The highest known cervical counts are in the extinct dolichosaurs where 19 cervical vertebrae have been recorded in the genus *Dolichosaurus longicollis* (Caldwell, 2000), and increased cervical counts seem to be common within this specialist group. Cervical numbers in snakes are, of course, unknown. Early in the history of squamates, the intervertebral joints became more sophisticated with the development of a posterior condyle meeting an anterior cotyle (procoely) and, in many groups (especially snakes), an elaboration of the accessory zygosphene-zygantrum joints that supplement the zygapophyses. Gekkonid geckos revert to amphicoely, probably as a consequence of paedomorphy. Most squamates retain intercentra, but these vary in number (from a minimum in *Heloderma* to a maximum in geckos), in size (from simple bars to deep hypapophyses, e.g. in snakes and varanids), and in position (from intercentral, e.g. most gekkotans, to mid-central, e.g. snakes and varanids). Similarly, the number and pattern of cervical ribs varies, but usually with the loss of ribs on anterior cervicals, a reduction in length in the mid-section, and longer ribs on the one or two vertebrae closest to the pectoral girdle (Hoffstetter and Gasc, 1969). The rare and secretive dibamids are unique amongst squamates in having ribs on the axis.

Changes in the basic morphology of the occipital surface of the skull have been generally less profound, but the kinetic potential of the skull may be

important to an understanding of the structure and arrangement of the muscles. In squamates, and perhaps primitively also in rhynchocephalians, the braincase is capable of movement in relation to the dermal skull (metakinesis), with joints at three points: between the paroccipital processes and lateral skull bones, the supraoccipital and parietal, and the basipterygoid processes of the basiphenoid and the pterygoid (Frazzetta, 1962). Squamates, but not rhynchocephalians, also have a mobility of the quadrate (streptostyly) in relation to the skull roof and palate, and many (but not all) squamates have an extra joint system between the frontal and parietal (mesokinesis).

1.A:3) Previous literature on the lepidosaurian craniocervical region

Research by many authors has contributed to today's knowledge of reptiles. However, no detailed review of the craniocervical region of squamates exists. This fact was the impetus for my thesis. The osteology of the cranium and the vertebral column in reptiles have been investigated by several authors: Baur (1886) studied osteology (e.g. the axial skeleton in chamaeleons); Broom (1925) investigated the cranial morphology of *Sphenodon*, agamids, chamaeleons, and gekkotans; Goodrich (1930) examined vertebral structure generally (e.g. the proatlas in crocodiles); and Romer (1956) discussed both the osteology and the myology of the neck and trunk in reptiles. A detailed description of the axial skeleton in reptiles was formulated by Hoffstetter and Gasc (1969), while Bellairs (1969) published on the osteology of the skull, the vertebral column and the pectoral girdle in reptiles (e.g. in chamaeleons, varanids, limbless anguids, amphisbaenians and snakes). Both Guibé (1970) and Paranjape

(1974) provided details of the craniocervical and the pectoral girdle musculature.

A large number of studies have been made on more specific groups. Mook (1921), and Wermuth (1953) studied the osteology of the crocodile skull, while Seidel (1978), looked into the osteology and morphology of the cervical region (e.g. *Alligator mississipiensis*). Iordansky (1964, 1973) investigated crocodilian skull morphology and jaw muscles (e.g. the shape of the lateral skull components, the attachment of depressor mandibulae, and the insertion of longus colli on the skull).

The osteology of the vertebral column in *Sphenodon* (e.g. the proatlas, and the number of cervical vertebrae and ribs) was studied by Albrecht (1883), Osborn (1903) and Howes and Swinnerton (1901). Byerly (1925) examined the myology of *Sphenodon punctatus*. Other workers have published on fossil taxa including Evans (1981) on the osteology of the cranium, vertebral column and pectoral girdle of *Gephyrosaurus bridensis*; Whiteside (1986) on *Diphydontosaurus;* and Fraser (1988) on *Clevosaurus*.

Cope (1892) studied the general osteology of lizards (e.g. the vertebral column of lacertids, amphisbaenians and xenosaurs), while Broom (1925) examined agamids, chamaeleonids, and the gekkonids. Camp (1923) made a comparative study of the head skeleton of lizards, while Jollie (1960) published details of the lizard skull. McDowell and Bogert (1954), described the cranial osteology of anguimorphs and Gekkota. Estes et al. (1988) brought together the results from a number of morphological studies of the cranium, the vertebral column and the pectoral girdle in a review of squamate relationships.

Iguanian cranial osteology was studied by Nopcsa (1928) and De Queiroz (1987) (iguanines), while Oelrich (1956) described cranial osteology as well as throat muscles (*Ctenosaura pectinata*), and Etheridge (1964) provided details of both the vertebral column and the ribs (*Sceloporus*). Blanc (1965) provided a detailed study of the osteology of the cranial and cervical vertebrae of *Chalarodon madagascariensis*. Frost and Etheridge (1989) focused on the osteology of iguanians, while Frost (1992) made a comparative systematic study of the iguanian skull, vertebral column and pectoral girdle. Beddard (1905) provided an account of cranial osteology in *Uromastyx*, and further information on the skull, vertebral column and pectoral girdle of agamids was provided by El-Toubi (1945, 1947), Islam (1956), and Tilak (1964). The myology of the craniocervical region in *Uromastyx aegyptia* was studied in detail by Khalil et al. (1977), while Wahba et al. (1992a) examined *Agama mutabilis*. Rieppel (1981), Rieppel and Crumly (1997) and Necas (1999) focused on the cranial osteology of chamaeleons, while Mivart (1870) and Wahba et al. (1992b) studied the myology of the craniocervical region.

The osteology of the skull and the vertebral column in geckos was described by Mahendra (1950) and El-Toubi and Khalil (1955), while Underwood (1954), Ganguly and Mitra (1958) and Holder (1960) dealt with vertebral column alone, and Kluge (1967, 1987) focused on characters of the skull, the vertebral column and pectoral girdle phylogeny. Wahba et al. (1992c) investigated the myology of the neck region in *Tarentola annularis*, dealing in particular with the episternocleidomastoid and the

longissimus capitis, and the appendicular musculature was studied by Zaaf et al. (1999).

For Scincomorpha, El-Toubi (1938) studied the osteology of the presacral vertebral column in scincids, while Greer (1970) used the osteology of the skull and the pectoral girdle in scincid classification. The osteology of the cordylids was described in detail by Lécuru (1968) and by Hoffstetter and Gasc (1969), while Barbadillo and Barahona (1994) focused on the osteology of the vertebral column of lacertids.

Parker (1868) contributed early observations on the osteology of the pectoral girdle in anguids. Subsequently, Barrow and Smith (1947), and then Costelli and Hecht (1971) made a detailed study of the osteology of the cranium, presacral vertebral column and pectoral girdle of xenosaurids. Boulenger (1891) and Pregill et al. (1986) described the vertebral column in helodermatids, while Herrel and De Vree (1999) looked in detail at cervical muscles in the same group.

Various authors have covered aspects of lifestyle and morphology in relation to the mechanics of locomotion and have also dealt with anatomy, especially for limbless taxa (Gray and Lisbon, 1950; Gasc, 1967; Webb et al., 1978; Young, 1981; and King, 1996). Essex (1927), Gasc (1981), and Gans (1985) investigated the axial musculature in limbless reptiles and its relation to locomotion. Gray (1946), Gray and Lissmann (1950) and Lissmann (1950) described the types and mechanics of locomotion in snakes, with more recent work on the same topic by Shine (1992).

Gans (1960, 1969a, 1973a,b, 1978, 1985) also observed limbless squamates, particularly with respect to the osteology and function of the cranium and

the vertebral column in amphisbaenians. Zangerl (1944, 1945) and Kritzinger (1946) studied cranial osteology and the vertebral column of amphisbaenians, and Al-Nassar (1976) made study of the amphisbaenian *Diplometopon zarudnyi*. Bellairs and Underwood (1951) examined the osteology of the vertebral column and ribs in both amphisbaenians and snakes

For snakes, the osteology of the cranium was described by Brock (1932) (e.g. *Glauconia nigricans*) and Gans (1973a) (uropeltid), also Gans (1962) studied the osteology of the vertebral column. Hoffstetter and Gayrard (1964) and Parker (1977) discussed both the skull and the vertebral column. Mosauer (1935), Sood (1948), Gasc (1967) and Auffenberg (1962) investigated the myology of the axial skeleton in snakes.

For other limbless taxa, Gasc and Gans (1990), described the osteology of *Anguis fragilis*, while Gans and Fusari (1994) reviewed the locomotion of other limbless squamates, including the osteology of reduced limbed scincids. Rieppel (1984) described the osteology and the morphology of the cranium in dibamids.

Aspects of craniocervical anatomy have also been discussed in the context of phylogenetic analysis, most notably by Evans (1988) and Gauthier et al. (1988) for basal Lepidosauromorpha and lepidosaurs; Estes et al. (1988) and Rieppel (1988; 1993) for Squamata; Etheridge and de Queiroz (1988) for iguanians; Grismer (1988) for eublepharid geckos; Abdala and Moro (1996), and Moro and Abdala (1998) for Gekkonidae; Gao and Norell (1998) for extinct Anguiomorpha; and finally, Lee (1997, 1998) and Caldwell (2000) for extinct varanoids and snakes.

1.A:4) Aims of this study

As noted above, the development of a mobile neck was a key feature in the evolution of amniotes. The cervical vertebrae and their musculature are relatively well studied in humans (e.g. Clemente, 1985; Agur et al., 1991; Warfel, 1993; Netter, 1998), other mammals (Rinker, 1954; Bekele, 1983; Richmond and Armstrong, 1988; Filan, 1990; Jouffory, 1992), archosaurs (Mook, 1921; Reese, 1923; Wermuth, 1953; Iordansky, 1964, 1973; Seidel, 1978; Murakami, 1988; Murakami et al., 1991; Cleuren and De Vree, 2000), birds (Kuroda, 1962; Zusi, 1985; Berge and Zweers, 1993; Zweers et al., 1994) and turtles (Ruckes, 1929; Williams, 1950; George and Shah, 1954, 1955; Shah, 1963).

However for most lizards, the cervical region is poorly known and has never been subjected to detailed comparative studies, as have other posterior epaxial muscles (Oelrich, 1956). Rieppel (1980) did consider the presence, position and orientation of the cervical muscles in the classification of anguimorph lizards, but only to a limited extent.

Of more than 6,000 species of the Squamata, only a relatively small sample were available for detailed destructive study. Allowing also for time constraints, I had to limit my examination to a sample which I hope will be as representative as possible, attempting at least to initiate an understanding of this important region (including the occipital region of the skull, the cervical vertebrae, the pectoral girdle and the muscles associated with them). The main aims of the study were as follows:

- A detailed comparative study of the anatomy (osteology and myology) of the craniocervical region of a representative sample of squamate taxa, with both *Sphenodon* and *Caiman* used for outgroup comparison.

- An understanding of the relationship between muscles and bone in this region, so as to provide a better interpretation of features present in dry or fossilised skeletons.

- Identification of unique, or at least characteristic, features for major clades.

- Identification of characters showing high levels of variation within and between taxa.

- A discussion of the distribution of craniocervical character states among different groups of Lepidosauria.

CHAPTER (1)

1.B) Section

General description and terminology of bones and muscles

1. B:1) Bones

Bones, cartilage and ligaments form the framework of the skeleton. In reptiles, they maintain the attachment of muscles and protect the body cavities. The endoskeleton is divided into an axial skeleton and an appendicular skeleton. The axial skeleton is composed of the skull, vertebral column, sternum and ribs; and the appendicular skeleton is composed of anterior and posterior extremities and the bones connecting them to the body axis, the pectoral girdle and the pelvic girdle. Bones contact each other in different ways, the point of articulation is called a joint. There are immovable joints, such as the sutures between parietal and squamosal or exoccipital and basioccipital on the skull, and between the hypapophyses and centra on the anterior presacral vertebrae. The slightly movable joints include the articulations between vertebral zygapophyses, and between adjacent centra. The freely movable joints occur between the components of the forelimbs and hind limbs, and their respective pectoral and pelvic girdles.

Cartilage is a flexible connective tissue that either lines the joints between bones, or forms the endoskeleton of the embryo that is replaced by bone in the adult stage. Some of this cartilage lasts in particular areas in reptiles, for example, the suprascapula, the distal tips of cervical and trunk ribs, and the uncinate processes.

Ligaments are mostly elastic flexible straps that hold two or more bones together at a movable joint. They control the position of the bones at the joint and prevent dislocation. In reptiles, ligaments may be found connecting the rib/transverse process and intercentrum, along the

centrum ventrally, connecting proatlas and exoccipital, atlas and occipital condyle, and between adjacent neural spines dorsally.

This work focuses on the craniocervical region of reptiles, including the occipital surface of the skull , the presacral vertebral column (cervical and anterior trunk vertebrae, ribs, sternum), and the pectoral girdle.

Skull

The first component of the axial skeleton is the skull. The relevant area of the skull is the posterior (occipital) surface, and the articular of the lower jaw. The important bones within this area are :

parietal, squamosal, supratemporal, quadrate, articular, supraoccipital, oto-occipital (fused exoccipital + opisthotic), quadrate and paroccipital epiphyses, and basioccipital (Diagram, 1.B:1.1).

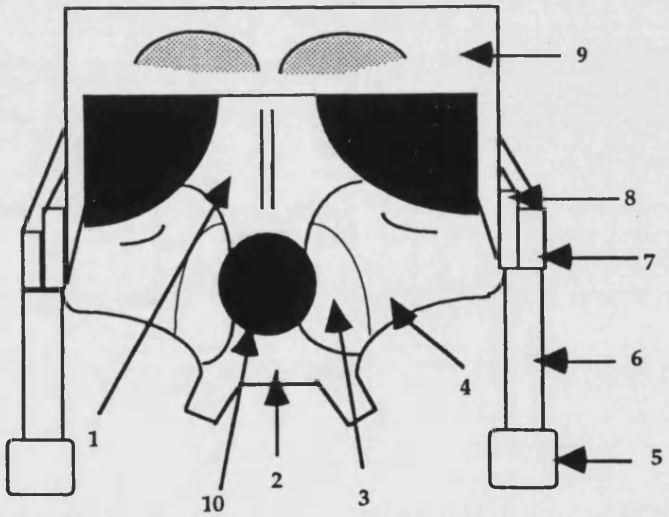


Diagram (1.B:1.1) occipital view of the skull.

1 = supraoccipital	5 = articular
2 = basioccipital	6 = quadrate
3 = exoccipital	7 = squamosal
4 = opisthotic with paroccipital process	8 = supratemporal
3+4= oto-occipital	9 = parietal
	10 = foramen magnum

1- Parietal:

A flat or dome-shaped bone that forms the posterodorsal roof of the cranium. The median parietal is unpaired in *Sphenodon* , and most

squamates except Gekkonidae (Camp, 1923; Mahendra, 1949; El-Toubi and Khalil, 1952), most pygopodids and xantusiids (Romer, 1956; Savage, 1963; Rieppel, 1984; Estes et al., 1988). In some taxa (e.g. *Phrynosoma* - family Iguanidae) the parietal and squamosal have horns and tuberosities (Reeve, 1952; Presch, 1969). Posteriorly, the parietal possesses two processes that extend posterolaterally towards the paroccipital processes, and contribute to the development of the large supratemporal fossa (Jollie, 1960). In some genera the posterior processes are reduced or absent (e.g. Chamaeleonidae, Fig. 1.B:1.1a), and are replaced by the squamosal.

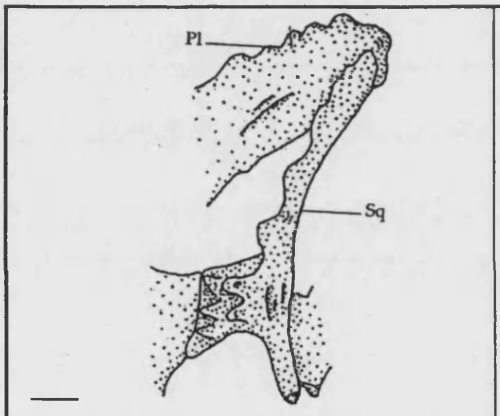


Fig. (1.B:1.1a) left lateral view of the skull where the parietal posterior lateral processes are absent in *Chamaeleo jacksonii*. . Scale bar = 1 mm.

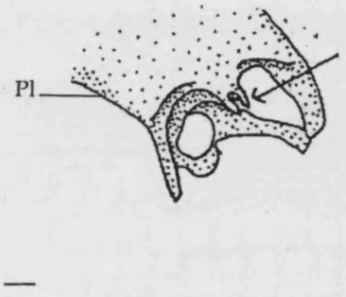


Fig. (1.B:1b) Left lateral view of the skull showing the forked mid-posterodorsal margin of the parietal in *Pseudocordylus microlepidotus*. Scale bar = 1 mm.

Generally, the distal ends of the posterior processes are narrow, but sometimes they are wide. The parietal contacts the frontal anterodorsally, and the squamosal and supratemporal posterolaterally. The posterolateral margin of the parietal varies. It is either smooth or embayed. Posterodorsally, the margin has paired concavities that differ in their depth, and shows traces of pits, fossae and bony elevations which reflect muscle attachment. The mid-posterodorsal margin may be smooth (most Squamata e.g. anguids), or possess a median process which is small (e.g. Gekkota), long, or sometimes forked (e.g. Cordylidae, Fig. 1.B:1.1b).

Ventrally, the bone meets the supraoccipital and sometimes bears an inferior crista (e.g. chamaeleons).

2) Squamosal:

This is an outer curved bone that is located above the quadrate and anterior to the paroccipital process (Goodrich, 1930; McDowell and Bogert, 1954; Romer, 1956). It either meets or does not meet the paroccipital process. The squamosal varies from a large quadriradiate or triradiate bone, to a narrow curved splint (most Squamata e.g. *Diplodactylus caudicinctus* - Fig. 1.B:1.2a). The posterior tip of the narrow squamosal may possess a ventral process which is either strongly or slightly curved. In some genera it retains a dorsal process (pointed or wide), which may meet the parietal (Agamidae*, e.g. *Uromastyx aegyptia*- Beddard, 1905, Fig. 1.B:1.2b). The squamosal sometimes retains both dorsal and ventral processes which vary in length (dorsal > ventral, dorsal < ventral, dorsal = ventral). The squamosal meets the postorbital to enclose the upper temporal fossa. In some groups it may be lost (e.g, gekkonids, pygopodids and amphisbaenians - Romer, 1956).

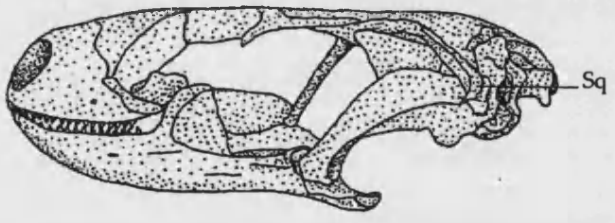


Fig. (1.B:1.2a) Left lateral view of the skull showing the squamosal (Sq)with splint-shaped narrow process in *Diplodactylus caudicinctus*. Scale bar = 1 mm.

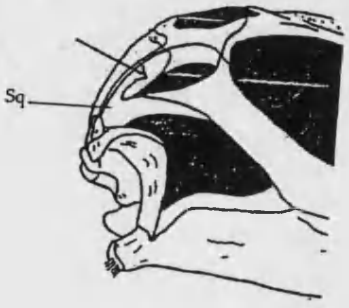


Fig. (1.B:1.2b) Right lateral view of the skull showing the squamosal (Sq) with dorsal process in *Uromastyx aegyptia*. Scale bar = 1 mm.

3) Supratemporal:

This is a flat bone which is either small or elongated (wide or narrow). If present, it is found between the parietal internally and the squamosal externally (Jollie, 1960). Both supratemporal and squamosal usually contact the quadrate, but in some genera such as gekkonids, only the supratemporal remains ("squamosal"as in Gaupp, 1900 - or "tabular" according to Broom, 1925; McDowell and Bogert, 1954). It is usually either longer or shorter (most Squamata, e.g. *Lacerta trilineata*) than the squamosal, but sometimes they are equal (some Agamidae*).

The supratemporal may extend along the lateral edge of the parietal (Gekkota) and sometimes runs posteriorly under it (Varanidae), or laterally along the paroccipital process (Helodermatidae). It may be reduced to a small flat splint close to the quadrate and otic capsule (Chamaeleonidae), or be absent (*Sphenodon*). The supratemporal attaches directly to the paroccipital process when the posterior process of the parietal is shortened.

4) Quadrate:

This is a large irregular element that provides the articulation between the cranium and the mandible. In most lizards, the quadrate is free to move forward and backward (streptostyly) (Jollie, 1960; King, 1996). Usually, the dorsal condyle (wide or narrow) of the quadrate meets the squamosal, supratemporal, paroccipital process, and sometimes parietal, while the ventral condyle articulates with the articular.

5) Retroarticular process of the articular:

The articular forms the posterodorsal end of the mandible (Kingsley, 1905), providing a dorsal concavity for the base of the quadrate. Posteriorly, the retroarticular process carries a shallow bony depression where depressor muscles attach (Gans, 1966b). It is either well- developed (e.g. *Sphenodon* - Fig. 1.B:1.3), and most squamates) or reduced

(chamaeleons and some amphisbaenians (McDowell and Bogert, 1954; Jollie, 1960).

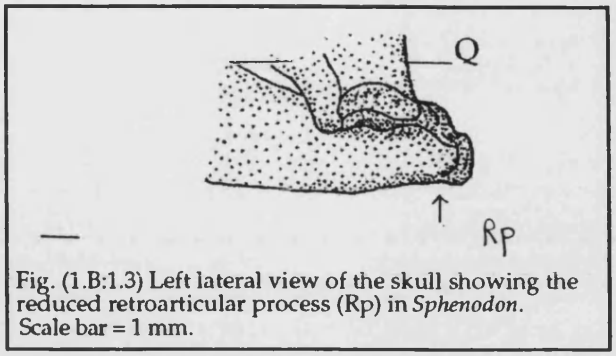


Fig. (1.B:1.3) Left lateral view of the skull showing the reduced retroarticular process (Rp) in *Sphenodon*. Scale bar = 1 mm.

6) Supraoccipital (epiotic):

This forms the dorsal roof of the foramen magnum and lies directly below the parietal. The anterior margin of the supraoccipital is separated from the parietal by a connective tissue gap (Jollie, 1960), but in some burrowers the gap is reduced (amphisbaenians and some skinks) or absent, and the supraoccipital and parietal are completely fused (e.g. *Acontias* - Brock, 1941; *Rhineura* - Zangerl, 1944). Ventrolaterally, the supraoccipital is sutured to the opisthotic and often the exoccipital. Anteriorly, its cartilaginous processus ascendens fits into a recess in the parietal (Jollie, 1960) (except in Gekkota, *Dibamus* and Pygopodidae, where it is absent - Rieppel, 1984). The bone may possess a long rounded median ridge, but some taxa the ridge is sharp (keeled) (e.g. *Oplurus cyclurus*). Alternatively, the surface may be smooth or possess a posterior crest (e.g. *Sphenodon* - where craniocervical muscles attach). Laterally, the supraoccipital margins are either smooth, or have a shallow ridge. In cordylids the supraoccipital has a median process that articulates with the posterior forked process of the parietal (Fig. 1.B:1.1b), while in *Chamaeleo* the supraoccipital possesses long sharp median processes (= inferior crista parietalis, Oelrich, 1956).

7) Oto-occipital (= fused exoccipital + opisthotic) :

This occupies the posterolateral part of the braincase. The exoccipital forms the lateral wall of the foramen magnum. In most genera, the exoccipital is sutured to the supraoccipital dorsally, and basioccipital ventrally (*Varanus*- Bahl, 1937; agamids - El-Toubi, 1947; *Hemidactylus* - Mahendra, 1949). Jollie (1960) noted the retention of a suture between the exoccipital and the supraoccipital (e.g. chamaeleons, varanids and anguids), or its disappearance (e.g. *Scincus, Iguana* and *Heloderma*). Greer (1985) related retention of the suture between the exoccipital and the supraoccipital, or the exoccipital and opisthotic to age. In *Sphenodon*, the opisthotic is sutured to the exoccipital (persists until the adult stage), but the bones are fused in most lizards (Jollie, 1960), with fusion occuring in the embryo (except dibamids, Estes et al., 1988; Gauthier et al., 1988). Such fusion results in a compound bone, the oto-occipital. The exoccipital is also separate from the basioccipital (e.g. dibamids - Greer, 1985; Iyer, 1943; Jollie, 1960).

The opisthotic has a strong lateral paroccipital process that meets the squamosal, supratemporal and quadrate. It may possess a sharp dorsal edge (where a deep muscle inserts), or is smooth. The ventrolateral margin of the oto-occipital is either concave, straight , or convex (e.g. Varanidae and gekkonids like *Hemidactylus flaviviridis* where ventral muscle slips insert. The margin either has a sharp edge (crista tuberalis - most Squamata), or is smooth. The ventrolateral tip of the oto-occipital near the basal tubera is convex (where a deep ventrolateral muscle inserts), straight, or concave. The ventral end of the oto-occipital near the border with the basioccipital is either smooth, or possesses a curved ridge (where the posterior intercentral muscles insert).

8) Paroccipital epiphyses:

The paroccipital epiphysis is a wedge-shaped cartilage, or an ossified extension which is connected to the external tip of the paroccipital

process (Rieppel, 1984). It is also called the intercalary (Jollie, 1960), and is either present or absent.

9) Basioccipital :

This forms the floor of the braincase and provides the central part of the tripartite occipital condyle (although, the condyle is not always tripartite [e.g. *Scincus*], and is formed by the basioccipital only - Kingsley, 1905; El-Toubi, 1938; Ramaswami, 1952). Anteriorly, the bone is united with the basisphenoid, while dorsally it sutured or fused with the exoccipital (Jollie, 1960). It has two ventrolateral basal tubera, each with one or two epiphyses. The epiphysis is either oval, triangular, or elongated (where deep ventral muscles insert). The central area between the basal tubera is either smooth, or possesses a thin ridge (where the superficial intercentrum muscle inserts).

The presacral vertebral column

The second component of the axial skeleton is the presacral vertebral column. It includes the cervical vertebrae, anterior trunk vertebrae and ribs. The cervical series includes the atlas, axis and up to seven additional vertebrae.

1) Proatlas and atlas (C1):

The proatlas is a small element that precedes the atlas, and is thought to be a protovertebral fragment (Devillers, 1954). Its presence is considered to be primitive (persists in early reptiles, *Sphenodon* and Crocodylia - Carroll, 1970). The proatlas is absent in squamates, although it was described in chamaeleons by Baur (1886), an observation I was not able to confirm. Hyman (1942) reported the presence of a little knob on the anterior side of the atlas in pygopodids, which might represent the pro-atlas.

The atlas is the first ring-like vertebra composed of paired atlantal arches and an intercentrum which joins the skull. The atlantal arch is a curved

dorsal structure with a posterior process. A transverse process gives attachment to pectoral girdle muscles in most Lepidosauria, but bears a short rib in the *Caiman* where most intermediate muscles insert. The intercentrum is either flat, or keeled (most Squamata, where the first intercentral muscle slip to the skull originates).

2) Axis (C2) :

This is the second cervical vertebra. The axis odontoid process rests on the atlas intercentrum (and = atlas centrum). The axis has a biconcave neural arch and possesses a posterodorsal process that is triangular or oval (where the splenius muscle attaches). The dorsal end of the axis spine is either keeled, or rounded (most Squamata, where deep craniocervical muscles originate). The squamate axis lacks true prezygapophyses, but has postzygapophyses. The dorsal surface of the postzygapophysis is smooth, has tubercles, or retains a posterior process (where the spinalis/semispinalis muscle attaches). The articulation between C2 and C3 makes an angle with the horizontal that is less, equal or greater than zero. The long, wide axis centrum has lateral transverse processes (where the iliocostalis muscle originates).

Ventrally, the centrum is either smooth or keeled (where deep ventral muscles extend). The axis possesses a second intercentrum which is either flat or keeled (where the second intercentral muscle to the skull originates). In some genera (e.g. *Gekko gecko* - Fig. 1.B:1.4), the base of the second keeled intercentrum possesses one or two small posterolateral lateral crests (where very deep ventral muscles insert). The axis contacts C3 ventrally with a sutured, or fused third keeled intercentrum, so the third keeled intercentrum is fused to C2, C3, or intercentral.

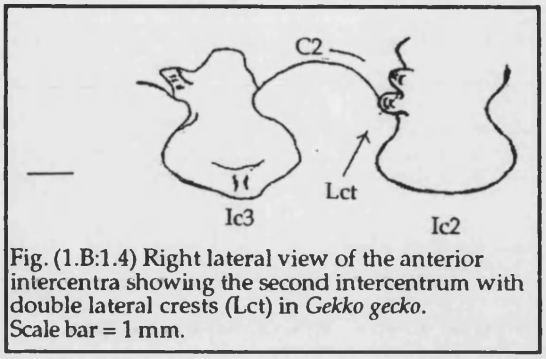


Fig. (1.B:1.4) Right lateral view of the anterior intercentra showing the second intercentrum with double lateral crests (Lct) in *Gekko gecko*. Scale bar = 1 mm.

3) C3 - C8-9 :

These are the anterior presacral vertebrae that precede the first dorsal vertebra (with the first rib that attaches to the sternum, Romer, 1956; Hoffstetter and Gasc, 1969).

Beddard (1905) defined the region as having a number of vertebrae with no ribs, but this is not correct. The number of cervical vertebrae varies from 5 - 9 (including the atlas and axis) and the number of the intercentra (hypapophyses) ventrally ranges from 2 - 8. Most squamates have 8 cervical vertebrae (Hoffstetter and Gasc, 1969).

The cervical neural spines are distinctive in their uniform shortness, and narrow tips, but they begin to get longer and wider posteriorly. The first tall cervical spine varies from C4 to C8 (where craniocervical muscle slips originate). The tips of the neural spines are either oval or triangular, while the height of the spines either increases (most squamates), decreases (burrowers) or remains the same posteriorly.

The posterior margins of the neural spines are either smooth (most Squamata) or wavy (e.g. *Sphenodon* - Fig. 1.B:1.5), and both anterior and posterior margins are either straight or curved (most Squamata).

Each vertebral arch possesses paired concave prezygapophyses anteriorly and convex postzygapophyses posteriorly. The prezygapophyses and postzygapophyses are either horizontal (=90°) (e.g. *Lacerta lepida asper*), or <90°. The postzygapophyses may be smooth, or bear either tubercles or a posterior process (e.g. *Sphenodon* - Fig. 1.B:1.6a).

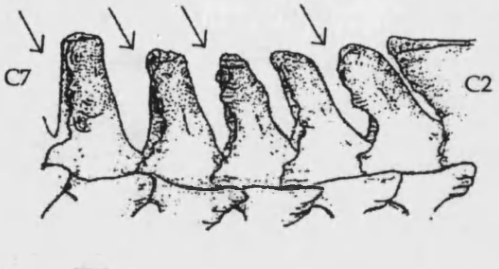


Fig. (1.B:1.5) Right lateral view of the cervical vertebrae showing the wavy posterior margin of the cervical spines in *Sphenodon*. Scale bar = 1 mm.

The prezygapophyses are either smooth externally (most Squamata), or possess a wide lateral ridge (= prezygapophyseal processes) (e.g. snakes and amphisbaenians - Hoffstetter and Gasc, 1969). In snakes, some iguanians and large lacertids the neural arch has an accessory facet known as a zygosphene which fits into a cavity in the preceding arch, the zygantrum (Fig. 1.B:1.6b). This articulation assists in stabilising the intervertebral articulations and prevents rotation of the spine along its axis (Gasc, 1967; Bellairs, 1969; Hoffstetter and Gasc, 1969). In many squamates, the zygosphene and zygantra are lost (Gauthier et al., 1988). The vertebral centrum/arch boundary possesses transverse processes where the cervical free ribs articulate.

The articulations between vertebral centra in the reptiles studied here may be divided into three types : procoelous, where a cotyle faces anteriorly and the convex condyle faces posteriorly (not developed in non-squamate lepidosauromorphs- Camp, 1923; Hoffstetter and Gasc, 1969; Estes et al., 1988) (Fig. 1.B:1.7); opisthocoelous where the cotyle faces posteriorly; and amphicoelous, with cotyles at each end (Camp, 1923; Nopcsa, 1930; Kluge, 1967; Wu et al., 1996) (Fig. 1.B:1.7). In adult squamates, the vertebrae are either procoelous or amphicoelous (Hoffstetter and Gasc, 1969), but in adult *Sphenodon* the vertebrae are amphicoelous (Holder, 1960; Kluge, 1987).

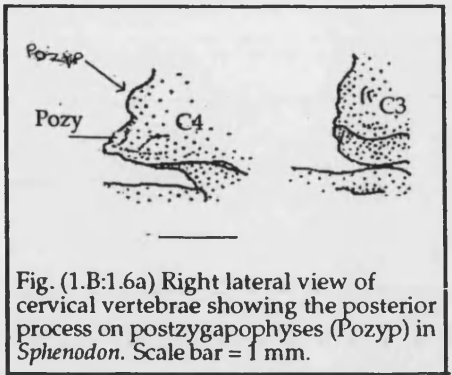


Fig. (1.B:1.6a) Right lateral view of cervical vertebrae showing the posterior process on postzygapophyses (Pozyp) in *Sphenodon*. Scale bar = 1 mm.

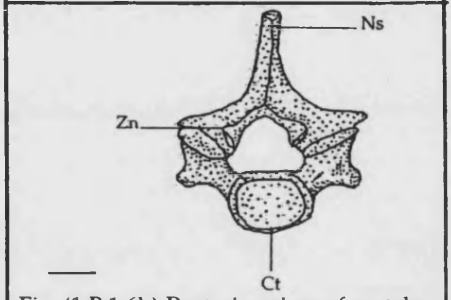


Fig. (1.B:1.6b) Posterior view of vertebra with zygosphene (Zn) in *Iguana iguana*. Scale bar = 1 mm.

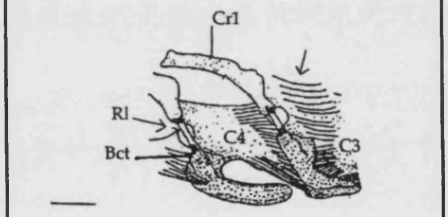
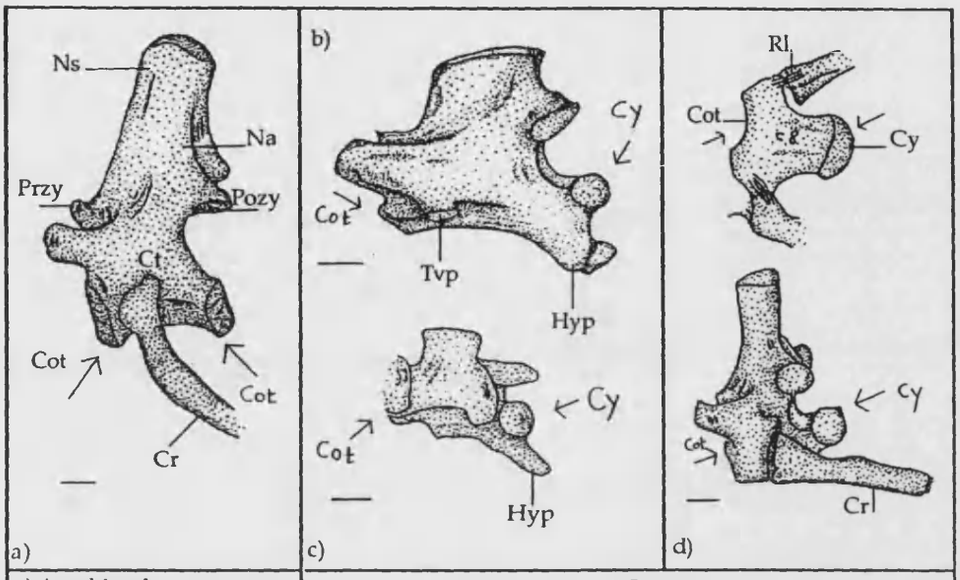


Fig. (1.B:1.6c) Right lateral view of the anterior intercentra showing the rib ligaments (Rl) between ribs & basal crests (Bct) in cervical region of the gekkonid *Gehyra marginata*. Scale bar = 1 mm.

Most squamates have procoelous vertebrae except many gekkonids (amphicoelous) (Underwood, 1954; Kluge, 1967; Moffat, 1973), although, eublepharids, pygopodids and most sphaerodactylines are procoelous (Noble, 1921; Holder, 1960; Kluge, 1967, 1987). Most authors agree that amphicoely is the primitive stem squamate condition, while procoely is advanced, with the condition in Gekkonidae as a reversal (Kluge, 1967, 1987; Moffat, 1973; Evans, 1981; Estes et al., 1988; Evans and Barbadillo, 1997; Reynoso, 1998). In primitive reptiles, small U-shaped bars of bone lie ventrally between the vertebral centra along the entire vertebral

column (Romer, 1956). In many more advanced reptiles, these intercentra are lost or reduced.



a) Amphicoelous.	b, c, d) Procoelous

Fig. (1.B:1.7) Left lateral view of vertebrae with amphicoely & procoely.
a) Sphenodon, b) Varanus prasinus, c) Trimeresurus albolabris, d) Heloderma horridum.
Cervical rib=Cr; Condyle=Cy; Cotyle=Cot; Hypapophysis=Hyp; Neural arch=Na; Neural spine=Ns; Postzygapophysis=Pozy; Prezygapophysis=Przy; Rib ligament=Rl; Transverse process=Tvp.Scale bar = 1 mm.

In crocodiles, the intercentra are generally absent, but the cervical centra retain ventral processes which are fused to the centrum behind (Hoffstetter and Gasc, 1969). *Sphenodon* retains the primitive condition, but in most squamates (except many Gekkota), intercentra are restricted to the cervical region (Hoffstetter and Gasc, 1969). Here they frequently develop keels. Strictly speaking, a hypapophysis is a ventral process on a vertebra or intercentrum, but there has been a tendency to refer to the keeled intercentra of the squamate neck as `hypapophyses'. This causes confusion if the intercentrum lacks a keel. For this reason, I use the terms intercentrum or keeled intercentrum for these structures, and use hypapophysis only for the sutured or fused ventral process in varanids or snakes.

Hypapophyses and intercentra are considered homologous, and keeled intercentra are characteristic of squamates (Osborn, 1900; Hoffstetter and Gasc, 1969; Gauthier et al., 1988). The intercentra may be shifted

forwards, backwards or fused with the centrum (Fig. 1.B:1. 8b & 8c) (Hoffstetter and Gasc, 1969). The intercentra are deep or shallow, and their number ranges between 2 - 10, although they may sometimes continue along the entire vertebral column (e.g. some snakes - Bellairs and Underwood, 1951). The shape of the intercentral apices varies from round to compressed, and they may bear lateral and central epiphyses (e.g. varanids, [Fig. 1.B:1. 8a] - Hoffstetter and Gasc, 1969). These keeled intercentra are usually free and held by ligaments. The ligament usually attaches to the intercentrum by a small posterior basal crest (e.g. *Gehyra marginata* - Fig. 1.B:1.6c). In addition, the keeled intercentrum may possess single or double posterior lateral crests close to the apex (for longus cervicus attachment). The cervical centra are usually short and typically bear a ventral keel, a feature which mostly decreases when the keeled intercentra disappear posteriorly.

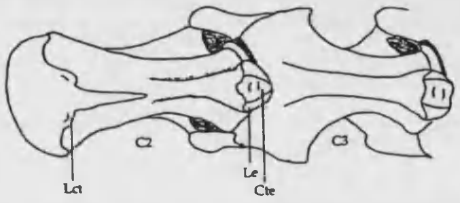


Fig. (1.B:1.8a) Right ventral view of anterior cervical vertebrae showing the hypapophyses with lateral (Le) & central epiphyses (Cte) in *Varanus griseus*. Scale bar = 1 mm.

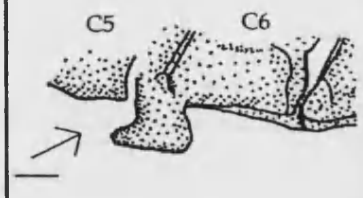


Fig. (1.B:1.8b) Left ventrolateral view of cerical vertebrae showing intercentrum 6 fused to the centrum behind in *Lacerta lepida pater*. Scale bar = 1 mm.

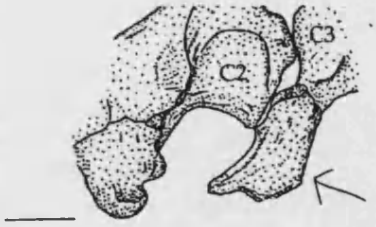


Fig. (1.B:1.8c) Left ventrolateral view of anterior cervical vertebrae showing intercentrum 3 sutured between two centra (C2-3) in *Gekko smithii* Scale bar = 1 mm.

4) Dorsal vertebrae:

These begin with the first vertebra having a rib that attaches to the sternum. The neural spine tips are either rounded or compressed and

their anterior margins are either curved or rather straight. The neural arch becomes wider with a uniform shape. The ribs are long and curved and the ventral surface of the centrum is longer, with no midline keel or hypapophyses (except in snakes). The first dorsal vertebral spine is slightly longer than that of the previous cervical vertebrae (where craniocervical muscle slips originate).

5) Ribs:

Ribs form laterally in the boundary between the epaxial and hypaxial muscles. In reptiles cervical vertebrae have short free ribs. These continue along the dorsal vertebrae as long curved structures with a cartilaginous section that attaches to the sternum. In squamates, all ribs articulate by a single-head (unicipital), but, in primitive lepidosauromorphs, two headed cervical ribs may be retained (Hoffstetter and Gasc, 1969) (e.g. the rhynchocephalian *Gephyrosaurus* , Evans, 1981). In archosauromorphs, two headed (bicipital) ribs are usually present on cervical vertebrae (Gauthier, 1984).

In squamates the number of cervical ribs ranges between 2 - 6. The first cervical rib is mostly without a cartilagenous end and articulates with one (most Squamata) or two heads (e.g. *Sphenodon*) on the transverse process (Hoffstetter and Gasc, 1969). The following cervical ribs may or may not possess a cartilaginous tip (Fig. 1.B:1.9b), and are either narrow, wide, or forked (where deep dorsolateral muscles attach).

The posterior cervical ribs articulate by a single head (except crocodiles where the first rib articulates with single head on C1, and posterior cervical ribs articulate with two heads - Hoffstetter and Gasc, 1969, Fig. 1.B:1.10a), and their shafts are either smooth, keeled, grooved, or bear crests (Fig. 1.B:1. 9a).

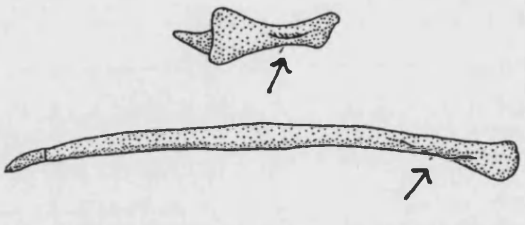


Fig. (1.B:1.9a) Cervical ribs with crests on the shaft in *Lacerta lepida pater*. Scale bar = 1 mm.

Fig. (1.B:1.9b) Cervical ribs with cartilaginous distal ends in *Heloderma horridum*. Scale bar = 1 mm.

Crocodiles and *Sphenodon* bear a tiny posterior extension on the dorsal ribs (= uncinate process) (Romer, 1956) (Fig. 1.B:1.10b). In limbless forms (e.g. *Ophisaurus*, *Anniella*, *Anguis* and *Dibamus*) the costal head has an outgrowth (pseudotuberculum), which may project posteriorly, anteroventrally, or both (symmetrical in *Dibamus*), while pygopodids have only the anteroventral process (Hoffstetter and Gasc, 1969).

In the following chapters, the rib pattern in the cervical region is expressed in the form of a ratio of: ribless cervicals + anterior short ribs + posterior long cervical rib. For example, in *Sphenodon* , ribs begin on C3. The C3 rib is short but is followed by four medium length ribs and one long rib, thus we get the formula of 2+1+4+1 (or as 2+1+5). In some limbless lizards the ribs are hard to separate into cervicals and dorsals because of the absence or reduction of the pectoral girdle, while in others like *Dibamus* the first rib articulates on the atlas or axis (Hoffstetter and Gasc, 1969).

6) Gastralia:

These are located ventrally, posterior to the sternum, and are composed of a series of rods connected together by connective tissue and superficial muscles. The sheet serves in protecting the lungs and abdominal viscera

(Romer, 1956). They are retained in many extinct reptiles (e.g. *Gephyrosaurus bridensis* - Evans, 1981), and the living *Sphenodon* and Crocodilia (Romer, 1956).

The pectoral girdle :

This is the part of the appendicular skeleton that connects the forelimbs to the trunk. It consists of the paired clavicles, scapulocoracoids and suprascapula, with the median interclavicle and sternum. It is well-developed in crocodiles and most lepidosaurs, reduced in limbless anguids, some skinks, Anniellidae, Dibamidae (Camp, 1923), and amphisbaenians, or absent, as in snakes.

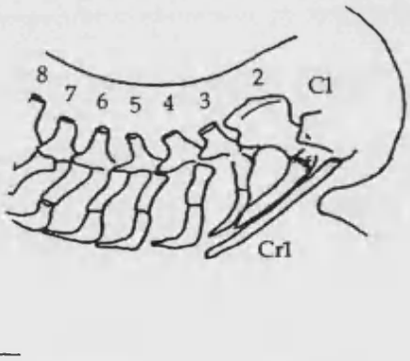


Fig. (1.B:1.10a) Right lateral view of the cervical ribs from C1 in *Caiman crocodilus*. Scale bar = 1 mm.

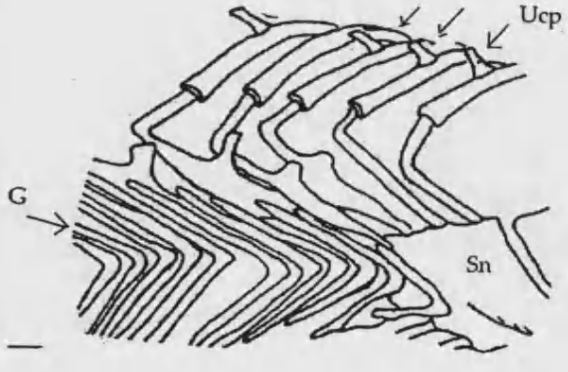


Fig. (1.B:1.10b) Right ventrolateral view of the pectoral girdle showing the uncinate processes (Ucp) on the dorsal ribs, and gastralia (G) in *Sphenodon*. Scale bar = 1 mm.

1) Sternum :

A cartilaginous flat unit that is found ventrally in the thorax, and is located between the pectoral girdle units such that the clavicles are anterior, the interclavicle is anteroventral, and the coracoids lie bilaterally. The sternum plays an important role with respect to the origin of one of the craniocervical muscles, episternocleidomastoid.

2) Clavicle :

This is a long, curved cylindrical bone that extends around the thorax anterior to the rib cage, and articulates by its acromial end with either the scapulocoracoid, suprascapula, or both. Ventrally its curved shaft attaches to the interclavicle via a narrow or wide, perforated end (e.g. xantusiids, Savage, 1963) (Diagram, 1.B:1.2). The clavicle and interclavicle undergo progressive reduction in various lineages, although Camp (1923) claimed that the clavicle always persists even if the pectoral girdle elements are absent (e.g. in anguimorphs where the scapulocoracoid and interclavicle are the first to disappear).

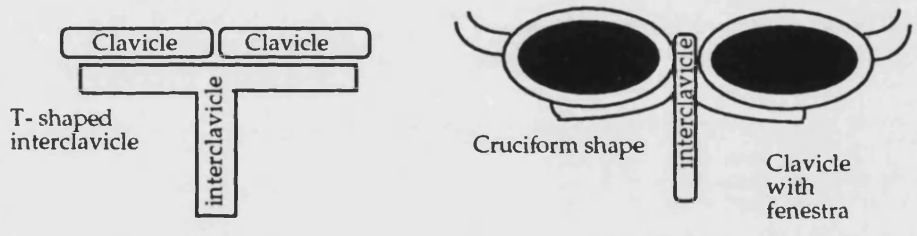


Diagram (1.B:1.2) ventral view of the pectoral girdle showing the various shapes of clavicle and interclavicle in Lepidosauria

3) Interclavicle :

This is a flat or curved bone located ventrally between the clavicles and the sternum. The interclavicle varies from T- shaped (*Gephyrosaurus* - Evans, 1981; *Youngina* - Gow, 1975; *Heleosaurus* - Carroll, 1976) with no anterior process, to cruciform (e.g. Scincomorpha - Camp, 1923; Gilmore, 1928; Barrows and Smith, 1947; Kluge, 1967, 1987; Lécuru, 1968; Greer, 1970; Costelli and Hecht, 1971), rod - like with no lateral arms (e.g. Helodermatidae - Lécuru, 1968); or absent (e.g. Chamaeleonidae, snakes,

amphisbaenians - Essex, 1927; Lécuru, 1968). In some fossil lizards such as *Scandensia ciervensis* from the Early Cretaceous of Spain, the interclavicle is rhomboid (Evans and Barbadillo, 1997).

4) Scapulocoracoid:

The scapula is a wide rectangular bone generally fused with the coracoid in the adult to form the scapulocoracoid. It articulates with the humerus at the glenoid cavity (fossa) posteriorly, and the clavicle anteriorly. The scapula has the cartilaginous suprascapula dorsally. In lateral view, the scapula is either wide with a shallow concavity (most Squamata) or narrow and cylindrical (e.g. chamaeleons - Skinner, 1959). The scapula gives attachment to a number of muscles that assist in the movement of the shoulder girdle and the forelimb.

The wide coracoid bone is fused to the scapula and contributes to the glenoid fossa for the humeral head. The bone may be solid, or have either one and two fenestrae.

5) Suprascapula :

A cartilaginous element that is continous with the dorsal margin of the scapula and extends towards the middorsal line. It is either a wide curved flat plate or a small crest (e.g. chamaeleons - Skinner, 1959). In some genera, the acromion of the clavicle articulates with the anterior edge of the suprascapula (e.g. *Uromastyx* - Islam, 1956). The suprascapula provides attachment for important muscles externally and internally that assist in pectoral girdle movement or connect it to the anterior vertebrae (e.g. atlas).

Table (1.B:1a) Bone terminology

- Skull

Bone name	Suggested names	Authors	Year
Basioccipital process	Tuberculum spheno-occipital	Jollie	1960
	Basal tubera	Jollie	1960
Paroccipital process	Mastoid process in mammal	Jollie	1960
Exoccipital	Occipital arches	Jollie	1960
	Exoccipitale	Oelrich	1956
Oto-occipital	= fused exoccipital & opisthotic	Jollie	1960
Processus ascendens	Processus anterior tecti	Jollie	1960
Quadrate	Os quadratum	Oelrich	1956
Squamosal + Supratemporal	Temporal bones	Jollie	1960
	Dorsal temporal element	Camp	1923
Parietal + Squamosal + Supratemporal	Post-temporal + Temporal arch units	Jollie	1960
Basioccipital	Processus basioccipitalis	Kalin	1933
	Os basioccipitale	Oelrich	1956
Supraoccipital	Os supraoccipitale	Oelrich	1956
Squamosal	Squamosal	Camp	1923
		Goodrich	1930
		Mc Dowell & Bogert	1954
		Romer	1956
	Paraquadrate	Gaupp	1900
	Squamosum	Oelrich	1956
Supratemporal	Supratemporal	Romer	1956
	Squamosal	Gauup	1900
	Tabulare	Broom	1925
		Brock	1932
	Tabular	Camp	1923
		Kluge	1967
	Supratemporale	Oelrich	1956

Bone name	Suggested names	Authors	Year
Parietal posterolateral processes	Parietal downgrowth	El-Toubi	1938
	Parietal posterior or cranial wall laminae	Jollie	1960
Posterior sagittal process	Crista parietalis inferior	Jollie	1960
		Rieppel	1987
		Rieppel & Crumly	1997
Quadrate epiphysis	Epiphysis of the quadrate	Siebenrock	1893
	Quadrate-jugal	Kingman	1932

- Table (1.B:1b) Presacral vertebral column

Bone name	Suggested names	Authors	Year
Prezygapophysis	Superior articular process	Clemente Agur et al.,	1985 1991
Postzygapophysis	Inferior articular process		
Neural spine	Spinous process		
Odontoid process	Dens		
Dorsal vertebrae	Thoracic and lumbar vertebrae		
Presacral vertebrae	Cervical + Thoracic + lumbar vertebrae		
Neural arch	Vertebral arch		
Centrum	Pleurocentrum	Hoffstetter and Gasc	1969
Atlas centrum	Odontoideum		
Atlantal arch	Neurapophyses	Islam	1956
Atlas posterior process	Postzygapophysis	El-Toubi	1938
		Barrows and Smith	1947
		Mahendra	1950
		El-Toubi and Khalil	1955
		Islam	1956
		Ganguly and Mitra	1958

Bone name	Suggested names	Authors	Year
Atlas intercentrum	Sub-vertebral wedge-bone	Reese	1923
	Ventral prominence	Mahendra	1936
	Atlantal hypapophyseal spine	Holder	1960
	Intercalary	Ganguly and Mitra	1958
	Atlantal intercentrum with median ventral hypophyseal process	Al-Nassar	1976
Atlas + Axis	Epistropheus	Romer	1956
		Islam	1956
Proatlas	Protovertebral fragment	Devilliers	1954
Intercentrum	Sub-vertebral widge-bone	Reese	1923
	Hypocentrum	Hoffstetter and Gasc	1969
Axis	Epistropheus	Islam	1956
Axis transverse process	Tuberosities	Zangerl	1945
Transverse process	Diapophysis Synapophysis	Romer	1956
Prezygapophyseal processes	Crescent lateral ridge	Al-Nassar	1976
Parapophysis + diapophysis	Synapophysis Paradiapophysis	Hoffstetter and Gasc	1969
Capitulum + tuberculum	Unicipital		
Chevron	Haemal arch	Romer	1956
Neural spine	Spinous crest neural spine	Hoffstetter and Gasc	1969
Presacral	Precloacal		
Rib	Pleurapophysis	Owen	1866
Dorsal ribs	Abdominal ribs	Camp	1923
Odontoid process	Dens epistrophei	Islam	1956

1. B:2) Muscles

The neck region has a number of muscles (fibres, sheets and bundles) which overlie the skeleton (posterior side of the skull, the cervical vertebrae and the pectoral girdle). According to their location and area of attachment, the neck muscles can be divided into two types: those designated intrinsic muscles (extending between parts of the axial skeleton) and extrinsic muscles (extending between the axial skeleton and the girdles with their limbs). The muscles that run dorsally above the level of the rib are called epaxial muscles, while the muscles that extend ventrally below the level of the rib are called hypaxial muscles. Laterally the vertebral transverse process and ribs separate epaxial and hypaxial muscles.

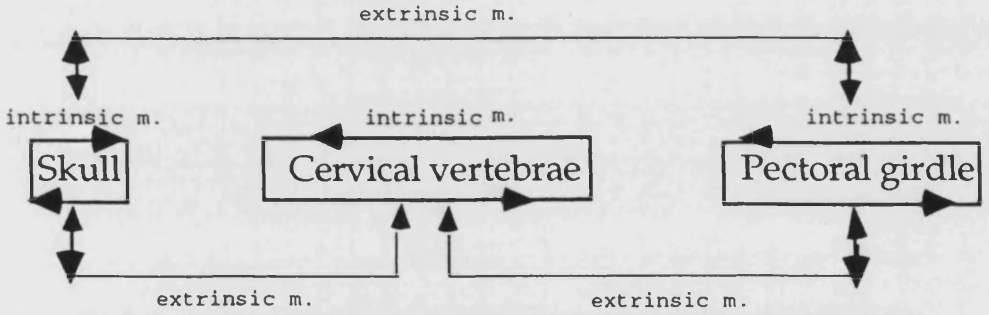


Diagram (1.B:2.1) showing muscle arrangment in the three skeletal parts that are related to the neck region.

Each muscle (intrinsic or extrinsic) has an origin where its point of attachment starts, and is fixed during contraction, while an insertion is where it ends and moves (Bellairs, 1969). Typically, a muscle leaves traces on the bone where it attaches, such as crests, ridges, rugosities, tubercles, depressions, concavities, convexities or roughened areas. Most muscles possess a tendinous sheet or bundle at the insertion area. At the same time, tendinous tissue may overlap the muscle bundle or connect muscle fibres to bone for strength and support. Muscles are divided into short muscles and long muscles. Short muscles are mostly thick and broad, while long muscles are usually thin and narrow, but can be complex (e.g. spinalis-semispinalis). A bundle may be oblique or

straight, broad and tapered, or narrow and strap-like. The fibres can be radiating or tapered (converging) from the area of origin or insertion. In this work, the neck muscles investigated are divided for description into 4 sections according to their arrangement (from the skin toward the bone surface) as follows: superficial muscles which lie directly under the skin; intermediate muscles, which appear after removing the superficial muscles; deep muscles, which form the bulk, occupy the inner surface along the cervical skeleton; and very deep muscles, which appear after removing the deep muscles and are directly in contact with the bone surface. Some superficial muscles extend posteriorly by originating from the occipital surface of the skull or the anterior cervical vertebrae (e.g. depressor mandibulae, cervicomandibulae), while others originate posteriorly from the middle and the posterior parts of the neck and the anterior part of the trunk region, and extend along the posterior cervical vertebrae and the anterior trunk vertebrae, (e.g. constrictor colli, trapezius, latissimus dorsi , iliocostalis rib muscles) .

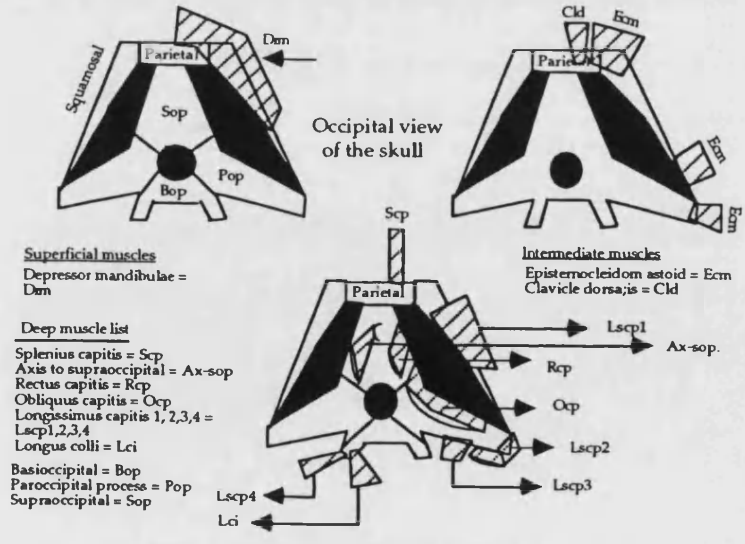


Diagram (1.B:2.2) Occipital view of the skull showing the superficial, intermediate and deep muscle insertion in *Sphenodon punctatus*.

Table (1.B:2a) superficial muscles around the neck and trunk region

Muscles	Origin and insertion
i) Depressor mandibulae internus and externus.	Originates from the skull and muscle fascia, and inserts on the dorsal side of the retroarticular process of the mandible (internus & externus slips).
ii) Cervicomandibularis	Originates posterior to the depressor mandibulae extenus from the muscle fascia dorsally, sometimes from the parietal, and inserts on the retroarticular process.
iii) Constrictor colli	Runs around the anterior and mid-neck region attaching to the muscle fascia.
iv) Trapezius	Originates from the muscle fascia, or neural spine tips dorsally, and inserts on the pectoral girdle laterally.
v) Latissimus dorsi	Originates from the mid-dorsal line (neural spine tips), and inserts on the humerus.
vi) Sub-iliocostalis rib muscles	See *Sphenodon.*

Table (1.B:2b) intermediate muscles along the neck region

These are extrinsic muscles connecting parts of the pectoral girdle to the skull or axial skeleton

Muscles	Origin and insertion
i) Episternocleidomastoid	Originates from the pectoral girdle ventrally, and inserts on the posterolateral side of the skull.
ii) Clavicle dorsalis	Originates from the dorsal muscle fascia (and sometimes the lateral skull components), and inserts on the anterior side of the clavicle laterally.
iii) Levator scapula ventralis Levator scapula dorsalis	Originate from the atlas transverse process, and both muscles insert on the suprascapula and scapula.
iv) Ribs to suprascapula/scapula (deep and superficial slips)	Originates from the distal end of the cervical and trunk ribs, and inserts on the anterior, middle and posterior inner surface of the suprascapula and scapula. The deep slips insert on the inner ventral edge of the suprascapula

Table (1.B:2c) deep muscles along the neck region

These are extrinsic and intrinsic muscles that run along the vertebral column and connect to the skull.

Muscles	Origin and insertion
i) Obliquus capitis internus + externus	Originates from the anterior cervical neural spines (externus).The internus covers further spines, and inserts on on the dorsal edge & ventrolateral surface of the oto-occipital.
ii) Rectus capitis	Originates from C1 and sometimes C2 neural spine, and inserts on the dorsal margin of the supraoccipital.
<u>Splenius capitis</u>	
i) Splenius capitis medialis + lateralis	Originates from the anterior tip of the cervical and dorsal neural spines (medialis), or muscle fascia (lateralis). The muscle inserts on the mid-posterodorsal side of the parietal.
ii) Splenius cervicus	Originates from the dorsal muscle bundles of splenius capitis, and inserts as muscle slips on the posterior dorsal edge of the cervical neural arch.
<u>Spinalis muscles</u> <u>Semispinalis muscles</u>	
i) Spinalis capitis	Originates from the anterior/posterior cervical neural spines, and inserts on the mid-posterodorsal side of the parietal under the splenius capitis origin.
ii) Spinalis /semispinalis cervicus (neck)	Originates above the cervical neural spines from the trunk spinalis/semispinalis complex, and runs anteriorly to insert as muscle slips on the posterior margin of the cervical neural spines and post-zygapophyses area.
iii) Spinalis/semispinalis complex (trunk)	Originates from the pelvic girdle, and extends anteriorly along the neural spines and arches of the presacral vertebrae. The spinalis attaches to the posterior tips of the neural spines, while the semispinalis attaches to the anterior tip of the neural spine. Both muscles cross above each other and run deep to fill the lateral concavity of the neural arch and zygapophyses area.
<u>Longissimus muscles</u>	
i) Longissimus dorsi	Originates from the ilium and sacrum, and runs anteriorly towards the skull by attaching to the zygapophyses laterally (muscle slips).
ii) Longissimus cervicus anterior + posterior	Branches from the deep longissimus dorsi along the anterior zygapophyses laterally, and inserts on the atlas posterior process (posterior). If a proatlas is present, the muscle branches end on it by an anterior slip (anterior).

Muscles	Origin and insertion
Longissimus capitis composed of :	The longissimus dorsi branches along the anterior cervical vertebrae to give the following bundles :
iii) Longissimus capitis ...1	Inserts on the parietal, exceptionally on the supraoccipital (chamaeleons) .
iv) Longissimus capitis...2	Inserts on the parietal, oto-occipital (lateral) and supratemporal.
v) Longissimus capitis ... 3	Inserts on the oto-occipital (ventrolateral) only.
vi) Longissimus capitis ...4	Inserts on oto-occipital (ventrally)/basioccipital, basioccipital only, mandible (amphisbaenian).
vii) Longissimus cervicus	Inserts on the atlas posterior process.
viii) Longissimus capitis minor	Branches from the longissimus cervicus along the atlas posterior process, and inserts on the oto-occipital ventrally.
<u>Iliocostalis muscles</u>	
i) Iliocostalis major	Originates posteriorly from the ilium and muscle fascia of the longissimus dorsi, and inserts on the axis transverse process. It inserts as slips of muscles from the rib shafts (iliocostalis externus and internus).
ii) Iliocostalis cervicus	Branches from the iliocostalis major along the axis, and runs anteriorly to insert on the outer edge of the atlas transverse process.
<u>Longus colli</u>	
i) Longus colli (centralis and lateralis)	Originates from the intercentra (or hypapophyses), rib ligament and centra of the anterior presacral vertebrae, and inserts on the basioccipital process (basal tubera). If inserts on the basal tubera = centralis If inserts on the oto-occipital= lateralis
ii) Longus cervicus	Originates posteriorly as muscle slips from the ligaments connecting the ribs to the intercentra, and inserts on the axis anterior intercentrum.
iii) Longus colli to iliocostalis	A short slip from the longus colli attaches to the iliocostalis along the 2nd cervical rib. See *Uroplatus.*

Muscles	Origin and insertion
i) Atlas to oto-occipital	Originates from the atlantal arch, and inserts on the dorsal side of the oto-occipital.
ii) Atlas transverse process to third cervical rib	See Iguanidae* .
iii) Atlas transverse process to paroccipital process and oto-occipital.	See Chamaeleonidae.
iv) Axis to supraoccipital	See *Sphenodon*
v) Axis to atlas neural arch.	Originates from the biconcave axis neural arch, and inserts on the posterior atlas neural arch.
vi) Quadrate to basioccipital	See Serpentes.
vii) Quadrate to parietal	See Serpentes.
viii) Clavicle to basioccipital	See *Anguis fragilis.*
ix) Cervical and trunk central tendon	A long tendon that runs along the centra and intercentra ventrally, usually it attaches to the last hypapophyses e.g. Gekkota.
x) Interspinalis	Short muscle slips that run between adjacent neural spines.
xi) Interneural arch	Muscle slips that extend above the interspinalis, and run between adjacent neural arches laterally (fill the concavities).
xii) Interzygapophyses	Run between adjacent zygapophyses as muscle slips. They are found below the interspinalis.

Muscles	Origin and insertion
Intercentral muscles	
i) First intercentrum to basioccipital (superficial) and oto-occipital (deep)	Originates from the first intercentrum, and inserts on the basioccipital central area or under the origin of the longus colli (superficial) and oto-occipital (deep).
ii) Posterior intercentra to skull (basioccipital & oto-occipital)	Originates from anterior intercentra of the cervical vertebrae, and inserts on both the basioccipital posterior border and the oto-occipital.
iii) Intercentra (posterior margins) to rib ligaments	Oblique slips that originate mostly from the posterior margins of the anterior intercentral bases, and insert on the anterior cervical rib ligaments. They appear after removing the longus cervicus (may be part of iliocostalis).
iv) Intercentral muscles (keeled intercentra)	A series of very deep short muscle slips that run along the hypapophyses tips.
v) Intercentra to suprascapula	Originates from the hypapophyseal apices, and inserts on the suprascapula anteriorly in Varanidae and some Anguidae.
vi) Hypapophyses to scapula and clavicle	See Varanidae.
vii) First or second intercentra to cervical ribs	See Anguidae.
viii) Intercentra to adjacent rib long muscles (cervical region)	See Chamaeleonidae.
ix) Intercentra to adjacent rib processes short muscles (run along the vertebral column)	See Amphisbaenia.
x) Posterior hypapophyses to anterior rib distal ends (run along vertebral column)	See Serpentes.
xi)Hypapophyses (posterior margins) to parapophysial processes (of transverse processes)	See Serpentes.
xii) Adjacent intercentra apices muscles	A number of muscle bundles that connect the intercentra apices laterally in Varanidae & some Gekkota.

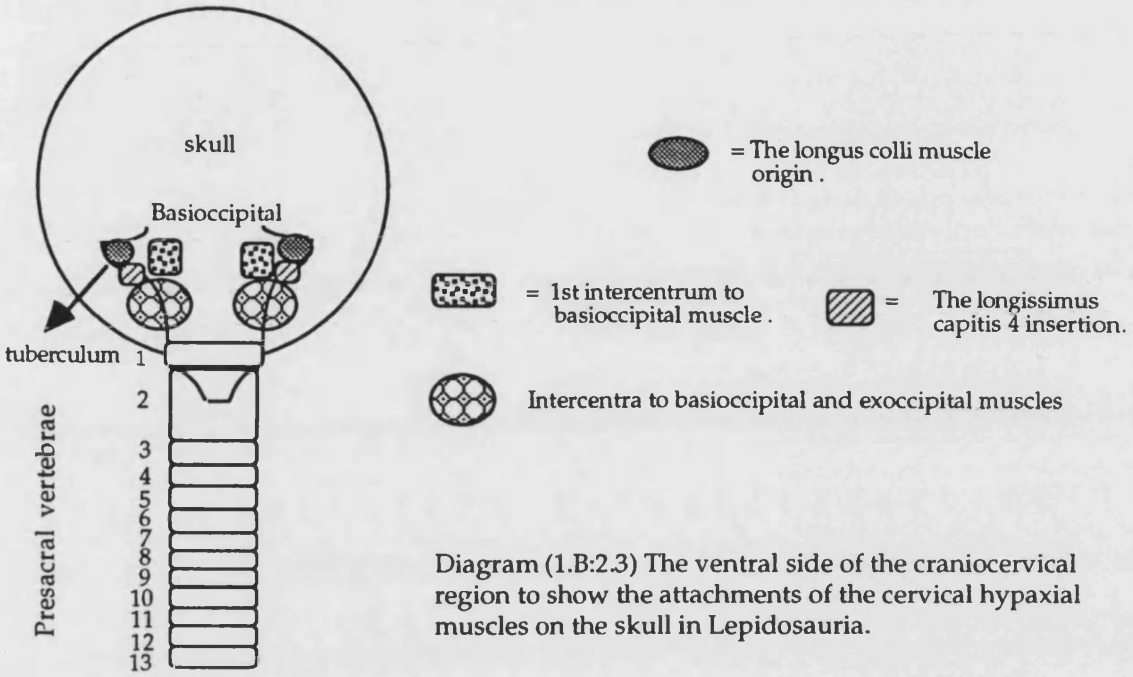


Diagram (1.B:2.3) The ventral side of the craniocervical region to show the attachments of the cervical hypaxial muscles on the skull in Lepidosauria.

Muscle terminology

Muscles have been named according to their origin, extension, size and location. As a result, authors have given alternative names for certain muscles:

1- Superficial muscles:

i) Depressor mandibulae (Haas, 1973; Paranjape, 1974).

Depressor mandibulae superficialis

(Guibé, 1970).

Depressor mandibulae posterior and anterior

(Moro and Abdala, 1998).

Muscle depressor mandibulae MDM and partes accessorius MDMA

(Herrel et al., 1998).

ii) Cervicomandibularis (Camp, 1923; Moro and Abdala, 1998).

iii) Constrictor colli (Camp, 1923).

Sphincter colli

(Romer, 1956; Guibe', 1970).

Intermandibularis posterior

(Moro and Abdala, 1998).

Constricteur du cou

(Guibé, 1970).

iv) Trapezius (Howell, 1936).

Curcularis

(Edgeworth, 1935).

v) Latissimus dorsi (Howell, 1936).

2- Intermediate muscles:

i) Sternocleidomastoideus (Howell, 1936; Moro and Abdala, 1998).

Sternocleidomastoidus

(Camp, 1923).

Sternocleidomastoid

(Romer, 1956; Paranjape, 1974; Wahba et al., 1992a,b,c)

Episternocleidomastoid

(Robinson, 1962).

ii)Levator Scapulae Superficialis and Levator Scapula Profundus (Howell, 1936; Guibé, 1970; Herrel and DeVree, 1999).

Levator scapulae

(Romer, 1956; Paranjape, 1974).

Levator scapula dorsalis and ventralis

Levator claviculae

(Mivart, 1870)

Suprascapula-atlas

(Wahba et al., 1992a,b,c)

iii) Suprascapula/scapula to ribs

Rhomboid muscles

(Agur et al., 1991).

Serratus

(Herrel and DeVree, 1999).

Serratus magnum

(Mivart, 1870).

3- Deep muscles:

i) Obliquus and rectus capitis (Guibé, 1970).

Rectus capitius posterior minor and major, Inferior oblique superior

(Agur et al., 1991)

Dorsal cranio-vertebral muscle (= rectus capitis)

(Clemente, 1985).

Lateral cranio-vertebral muscle (=obliquus capitis)

Clemente, 1985; Wahba et al., 1992a,b,c).

ii) Splenius capitis (Agur et al., 1991).

Spinalis capitis

(Romer, 1956).
Cranio-spinalis
(Wahba et al., 1992a,b,c).

iii) Spinalis capitis (Romer, 1956).
Semispinalis capitis
(Agur et al., 1991).
Splenius
(Romer, 1956).
Transversospinalis capitularis
(Guibé, 1970).
M. cervico-capitis medialis
(Gasc, 1981).

iv) Spinalis cervicus
Semispinalis cervicus
(Agur et al., 1991).
M. testo-cervicalis medialis
(Gasc, 1981).
Cervical inner semispinalis units
(Wahba et al., 1992a,b,c).

v) Spinalis/ semispinalis complex.
Transversospinalis
(Romer, 1956).
Spinalis thoracis
(Agur et al., 1991).

vi) Longissimus dorsi
Longissimus
George, 1948; Romer, 1956; Guibe´, 1970).
Metapophyses
(Mivart, 1870 - Mammalia).

vii) Longissimus capitis (Agur et al., 1991; Russell, 1967).
Suboccipitalis
(Guibé, 1970).
Suboccipital triangle
(Agur et al., 1991).
Longissimus capitularis superficialis and profundus
(Guibé, 1970).
Longissimus cervico-capitus
(Romer, 1956).

Cranio-costal
(Wahba et al., 1992a,b,c).
Iliocostalis capitis
Herrel and DeVree, 1999).
Transversalis capitis
(Oelrich, 1956).
Articulo parietalis = longissimus capitis 1, transversalis capitis = longissimus capitis 2, transversalis cervicis = longissimus capitis 4
(Nishi, 1916; Russell, 1967).
Articulo parietalis
(Herrel and DeVree, 1999).

viii) Longissimus cervicus (Clemente, 1985).
Cervical verebral adductor
(Wahba et al., 1992a,b,c).
M. interarticularis superior
(Gasc, 1981).

viii) Iliocostalis (George, 1948).
Costo-atlas
(Wahba et al., 1992a,b,c).

x) Longus colli (Smith, 1960).
Ventral cranio-vertebral
(Wahba et al., 1992a,b,c).

iv) Hypapophyses to rib distal ends
Hypapophyses to parapophyseal muscle slips
M. parapophys hypapophyseus
(Gasc, 1981).
in trunk, transversohypapophyseus
(Mosauer, 1935)

4- Very deep muscles:
Interspinalis (Agur et al., 1991)
Multifidus

ii) Interzygapophyses
Interarticulares
(Herrel and DeVree, 1999).

iii) Interneural arches
Interarcuales (Herrel and DeVree, 1999).

Names constructed for muscles, or parts of muscles that I identified during this study, but for which I could find no alternative name in the literature:

Clavicle dorsalis.
Atlas transverse process to cervical rib.
Splenius cervicus.
Longissimus cervicus anterior and posterior.
Longissimus capitis 1, 2, 3, 4.
Longissimus capitis minor.
Iliocostalis cervicus.
Longus cervicus.
Longus colli to iliocostalis.
Atlas transverse process to paroccipital + oto-occipital.
Axis to supraoccipital.
Axis to atlas neural arch.
Interneural arch.
Interzygapophyses.
Interhypapophyses.
Quadrate to basioccipital.
Quadrate to parietal.
Clavicle to basioccipital.
Cervical and trunk rib tendon.
First intercentrum to basioccipital and oto-occipital.
Posterior intercentra to basioccipital and oto-occipital.
Intercentra (or = hypapophyses) to cervical rib ligaments.
Intercentra (or = hypapophyses) to suprascapula.
Hypapophyses to scapulocoracoid/clavicle.
First or second hypapophyses to cervical ribs.
Hypapophyses to adjacent rib long muscles (cervical region).
Hypapophyses to adjacent rib processes short muscles.
Posterior hypapophyses to anterior rib distal ends (vertebral column).
Hypapophyses (posterior margin) to parapophysial processes.
Adjacent hypapophyses apices muscles.

1.C) Section

Materials and Methods

1.C:1) Dissection

The specimens used in this project came from Natural History Museum (NHM); from the Department of Anatomy and Developmental Biology at University College London (Prof. Susan Evans); from the Smithsonian Institution, Washington; and from the Royal Scottish Museum, Edinburgh. A small number of specimens were collected from Kuwait and Spain (see Appendix). All taxonomic names were checked for validity on the European Molecular Biology (EMBL) database. Where the original label name was no longer valid, it follows the current name in parentheses. There were two types of specimens: -

1- Dissected specimens: Most of the dissected specimens were formalin-fixed and transferred to 70% ethanol for dissection (except few taxa collected in Kuwait and Spain). Unfortunately, since some of the specimens had under gone post-mortem examination, some muscles were poorly preserved, rigid or destroyed particularly on the dorsal side, although most of the deep ventral muscles were well preserved. The dissection was done under a Wild stereomicroscope, fitted with a camera lucida for illustrations.

2- Skeletal specimens: Most osteological material from the NHM consisted of dry prepared skeletons, but I also examined some of the skeletal parts of the dissected specimens. All scales are in millimetres.

1.C:2) Character distribution

67 anatomical characters (osteological and myological) from the neck region were listed and a data matrix constructed using MacClade version 3.03 (Maddison and Maddison, 1992). Each listed character has several states coded from (0) possibly plesiomorphic to (5) etc, as needed (Maslin, 1952; Hennig, 1965; Crisci and Stuessy, 1980; Watrous and Wheeler, 1981). I used a phylogenetic tree based mainly on Estes et al. (1988), but recognising some of the controversial areas (e.g. the relationships of Gekkota, Scincomorpha and Anguimorpha). Other trees examined were those of Gaüthier et al. (1988), Caldwell, (1998), Lee (1997, 1998) and Reynoso (1998). For out-group comparison (Stevens, 1980; Watrous and Wheeler, 1981; Arnold, 1981; Farris, 1982; Maddison et al., 1984; De Queiroz, 1985; Estes et al., 1988; Gauthier et al., 1988; Frost and Attridge, 1989), I used a *Caiman* and the rhynchocephalian *Sphenodon*. This outgroup comparison was extended where possible using literature on birds, mammals and turtles.

Clearly, this is not a cladistic analysis since I have mapped my observed characters onto an existing tree in order to evaluate the potential of these characters for future analyses (with a complete data set) and also to see whether craniocervical characters reflect current ideas on the relationships of lepidosaurs.

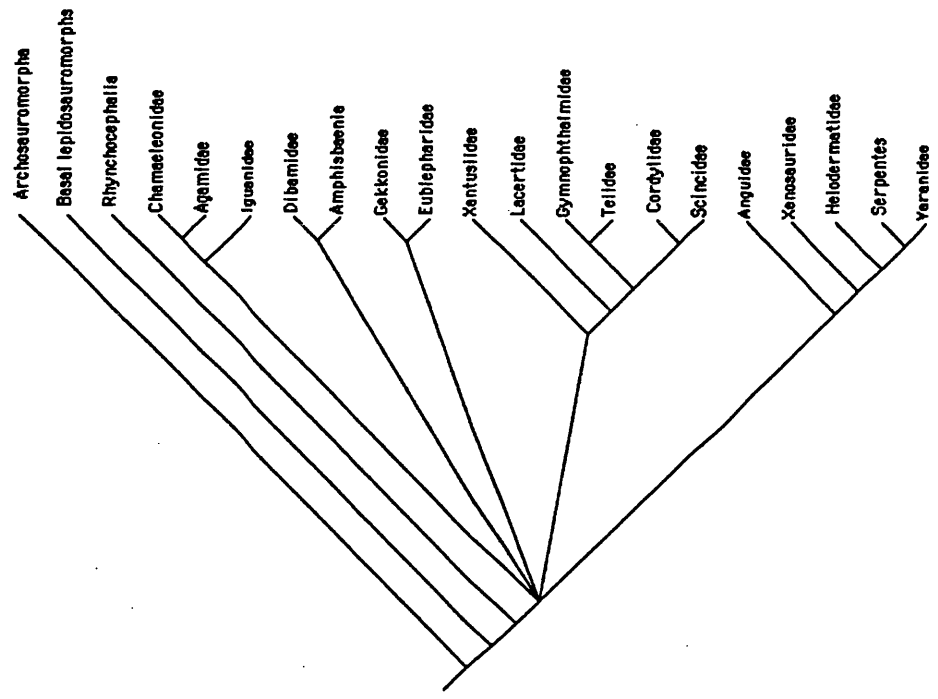


Fig. (1.C) a phylogenetic tree was constructed by other authors (e.g. Estes et al. 1988 and Gauthier et al., 1988) based on their observations and results. I used this tree for my craniocervical character distribution.

1.C:3) Species lists:

For some major clades, I made a detailed dissection of one representative such as: *Caiman crocodilus* which is an archosaurs that represents the out-group of lepidosaurs and belongs to the family Alligatoridae; *Sphenodon punctatus* which is the only living member of the Rhynchocephalia and belongs to the family Sphenodontidae; the limbless amphisbaenian *Diplometopon zarudnyi* from family Trogonophidae; and the snake *Trimeresurus*, family Viperidae. For more information, refer to the appendix.

Other species are listed on the following tables with their names and sources.

Species lists and sources of specimens:

Family: Alligatoridae.

Species name: *Caiman crocodilus* (dissected specimen).

Crocodylus niloticus (skeletal specimen).

Alligator mississipiensis (skeletal specimen).

The dissected specimen was from UCL, number 714/53, length = 152mm (no record of locality). The first skeletal specimen was from NHM, number 45, 3-29, 13, Africa, length = 245mm. The second skeletal specimen was also from NHM, number Coll 3, P. 290 (Zoological Society of London).

Family: Gekkonidae.

Species name: *Hemidactylus flaviviridis* (dissected specimen).

H. fasciatus (skeletal specimen).

The dissected specimen was from Kuwait (collected by Mr. S. Al Beshara from Al Edelia area, Kuwait City in 1994). The skeletal specimen, *H. fasciatus*, was from NHM, 1911.5.29.1 (Gold Coast).

Family: Trogonophidae.

Species name: *Diplometopon zarudnyi* (dissected specimen)

Trogonophis wiegmanni (skeletal specimen).

The dissection specimen was from Kuwait (collected by Mr. M. Al-Sayer, from Al-Wafra area, Kuwait/Saudi Arabian border). Length = 170 mm. The skeletal specimen was from NHM, male number 94.3.22-4, length = 135mm.

Family: Viperidae.

Species name: *Trimeresurus wagleri* (dissected specimen).

T. albolabris (skeletal specimen).

The dissected and skeletal specimens were from NHM. The skeletal specimen number is 215, and the length = 785mm.

Table (1.C:3a)

		GROUP IGUANIA	SOURCE		
			UCL	NHM	OTHER
IGUANIDAE*	Dissected specimens	*Oplurus cyclurus*	✓		
		Anolis richardii 1931.10.18.72-76-7.2/31. Tobago. L. = 105mm		✓	
		Iguana iguana (L. = 33cm.)	✓		
		Crotaphytus collaris	✓		
		Phrynosoma platyrhinos 3942, California.		✓	
	Skeletal specimens	*Anolis edwardsii* xx11.36.e, Jamaica. L. = 98mm.		✓	
		Anolis biporcatus 98.4.28.14, Ecuador. L.=75mm.		✓	
		Iguana iguana rhinopha 1974.2487. Nicaragua. L. = 250mm		✓	
		Crotaphytus collaris (no skull) 88.12.11.2, Texas			
		Phrynosoma asio 1903.9.30.112		✓	
AGAMIDAE*	Dissected specimens	*Uromastyx aegyptia microlepis* (baby). L. = 66mm.			✓
		U. aegyptia microlepis (adult). L. = 300mm.			✓
		Ceratophora stoddartii		✓	
		Moloch horridus			✓
		Draco fimbriatus 1967.2815, Malaya		✓	
		Calotes versicolor 98.12.22.1		✓	
		Phrynocephalus maculatus 1971.1651-BM 1971		✓	
		Agama agama 1962.1591.		✓	
		Pogona sp.	✓		
	Skeletal specimens	*Uromastyx aegyptia* 1849.8.23.4, Egypt.		✓	
		Moloch horridus 1910.5.28.10		✓	
		Draco spilopterus 1931.1.8.1 Gerrard		✓	
		Calotes versicolor 154.11, Ceylon		✓	
		Phrynocephalus mystaceus 90.9.22.22		✓	
		Agama agama 1969.687		✓	
		Pogona barbata 62.2.21.12		✓	
CHAMAELEONIDAE	Dissected specimens	*Chamaeleo chamaeleon* 1973,767-BM L. = 115mm.		✓	
		Chamaeleo jacksonii 1935.11.2.34		✓	
		Chamaelo vulgaris	✓		
		Chamaelo dilepis	✓		
	Skeletal specimens	*Chamaeleo jacksonii* 1910.10.31.8.		✓	
		Chamaeleo vulgaris 1920.1.20.1156		✓	
		Chamaeleo dilepis (no skull) 93.10.26.32.		✓	

UCL = University College London. NHM= Natural History Museum.

▒ = Species selected from each family for detailed description (bones, muscles)

Others includes:
Royal Scottish Museum Edinburgh, *M. horridus;* Smithsonian Museum, Washington, *Elgaria.*

Kuwait: *U. aegyptia microlepis.*

Iguanian taxa updated (from EMBL REPTILE database home page, maintained by Uetz,P.).

- *Uromastyx aegyptius microlepis* , changed and updated on 17 March 2001, to *Uromastyx aegyptia microlepis.*
- *Draco formosus* , changed and last updated 2001, to *Draco fimbriatus.*
- *Pogona barbatus,* changed and updated by 17 March, 2001, to *Pogona barbata..*
- *Chamaeleo jacksoni*, changed and updated on 26 Oct, 2000, to *Chamaeleo jacksonii..*

Table (1.C:3b)

	GROUP GEKKOTA		SOURCE		
			UCL	NHM	OTHER
DISSECTED SPECIMENS	*Hemidactylus flaviviridis*				✓
	Tarentola mauritanica				✓
	Phelsuma madagascariensis	L. = 95 mm	✓		
	Gekko gecko	L. = 235 mm	✓		
	Chondrodactylus angulifer	L. = 95 mm	✓		
	Ptychozoon kuhli	L. = 70 mm	✓		
	Uroplatus fimbriatus	L. = 105 mm	✓		
	Eublepharis macularis	L. = 110 mm			✓
SKELETAL SPECIMENS	*Hemidactylus fasciatus*	1911.5.29.1		✓	
	Ptychozoon kuhli	L. = 70 mm	✓		
	Tarentola mauritanica	(male - 1913.7.3.36) L. = 77 mm		✓	
	Phelsuma madagascariensis	(B.M. 85.6.4) L. = 95 mm		✓	
	Phelsuma guentheri	(B.M. 90.6.23.1) L. = 85 mm		✓	
	Gekko gecko			✓	
	Gekko smithii	(1908.12.28.28) L. = 151 mm		✓	
	Chondrodactylus angulifer	(male - 1910.4.20.2) L. = 74 mm		✓	
	Uroplatus fimbriatus	(61.3.20.9) L. = 145 mm		✓	
	Eublepharis macularis	(male - 87.11.2.3) L. = 60 mm		✓	
	Gehyra marginata	(male - 1910.4.26.9) L. = 94 mm		✓	
	Diplodactylus caudicinctus	(male - 1911.7.11.1) L. = 115 mm		✓	

UCL = University College London.
NHM = Natural History Museum.
Others includes specimens from
Kuwait: *H. flaviviridis*
Palma de Majorca, Spain: *T. mauritanica*
▩ = Species selected from each family for detailed description (bones, muscles)

Some gekkotan taxa are updated (from EMBL REPTILE database home page, maintained by Uetz, P.)

- *Uroplates fimbriatus; Eublepharius macularis; Gekko smithi; Psilodactylus caudicinctus* were updated: 17 Jan 2002, to *Uroplatus fimbriatus; Eublepharis macularis; Gekko smithii; Diplodactylus caudicinctus.*

Table (1.C:3c)

GROUP SCINCOMORPHA			SOURCE		
			UCL	NHM	OTHER
F. Scincidae	Dissected	*Scincus mitranus* BM 1973, 2088-2103, UAE. , L.= 100mm.		✓	
		Scincus alifasciatus laterimaculatus		✓	
		Tiliqua nigrolutea	✓		
		Tiliqua rugosas	✓		
	Skeletal	*Scincus fasciatus* 1906. 5. 7. 5. Tokota.		✓	
		Tiliqua nigrolutea 471, Australia. Zoological Socity of London.		✓	
		Tiliqua rugosas 299. Vol, 3, p. 143. (ZSL).		✓	
F. Lacertidae	Dissected	*Lacerta trilineata* South east Europe. L. = 130 mm		✓	
		Acanthodactylus boskianus asper		✓	
	Skeletal	*Lacerta lepida pater* 1920. 1. 20. 1259		✓	
		Acanthodactylus boskianus asper 95. 5. 23-46 Aden Female		✓	
F. Teiidae	Dissected	*Ameiva ameiva* 1946, 4.3.25. L. = 100mm		✓	
		Kentropyx calcarata		✓	
	Skeletal	*Ameiva ameiva* Vol. 2. p. 352/93		✓	
		Kentropyx calcarata 1902. 5. 29. 91/ Bolinia		✓	
F. Cordylidae	Dissected	*Cordylus polyzonus* BM 1988.557 - Namagualand. L.= 95 mm		✓	
		Gerrhosaurus flavigularis			✓
		Cordylus warreni			✓
	Skeletal	*Pseudocordylus microlepidotus* Vol 2/64. 2.2, 27 S. Africa		✓	
		Gerrhosaurus flavigularis 63. 2. 21. 30 S. Africa		✓	

UCL = University College London.
NHM = Natural History Museum.
▨ = Species selected from each family for detailed description (bones, muscles)

Scincomorphs taxa updated (from EMBL REPTILE, database home page, maintained by Uetz, P.).

- *Scincus mitrunus*, created 31 Jan. 1996/ last updated on 18 July 2001, to *Scincus mitranus*.
- *Acanthodactylus baskianus asper* created: 9 March 1996/ last changed or updated 17 March 2001, to *Acanthodactylus boskianus asper*.
- *Kentropyx calcaratus* created: 14 Feb, 1996/ last changed or updated on 6 September 2001, to *Kentropyx calcarata*.
- *Pseudocordylus microlepidetus* created: 19 Jan 1996, last changed or updated on 6 Nov. 2000, to *Pseudocordylus microlepidotus*.

Table (1.C:3d)

GROUP ANGUIMORPHA				SOURCE		
				UCL	NHM	OTHER
F.Varanidae	Dissected	*Varanus griseus*		✓		
		Varanus doreanus		✓		
		Varanus jobiensis		✓		
	Skeletal	*Varanus gilleni*	BMNH 1910.5.28.13		✓	
		Varanus griseus	BMNH 1974.24.83.N		✓	
		Varanus prasinus	78.10.16.38		✓	
F. Helodermatidae	Dissected	*Heloderma horridum*		✓		
	Skeletal	*Heloderma horridum*	(MALE) 1969.830 Mexico		✓	
F. Xenosauridae	Dissected	*Shinisaurus crocodilurus*		✓		
	Skeletal	*Shinisaurus crocodilurus*				
F. Anguidae	Well-developed limbs, Dissected	*Elgaria multicarinata*				✓
	Well-developed limbs, Skeletal	*Gerrhonotus imbricatus*			✓	
	Short limbed, Dissected	*Diploglossus crusculus crusculus*			✓	
	Short limbed, Skeletal	*D. monotropis*	1910.6.27.4, Ecuador		✓	
		D. shamini	63.2.21.1 y		✓	
	Limbless, Dissected	*Ophiodes intermedius*	2x297 a. No. 1962.9		✓	
		Anguis fragilis	skull=1908.5.29.24, cervical region 2424 xxxvII. Trukey.		✓	
	Limbless, Skeletal	*Ophiodes striatus*	44.3.7 - 63, Brazil		✓	
		Anguis fragilis	1920.1.20.2728		✓	

UCL = University College London.
NHM = Natural History Museum.
Smithsonian, Washington, USA.
▒ = Species selected from each family for detailed description (bones, muscles)

One anguimorph taxon updated (from EMBL REPTILE, database home page, maintained by Uetz, P.).
- *Diploglossus monotrofis* created on 27 Jan 1996 / last updated on: 6 Nov. 2000, to *Diploglossus monotropis*.

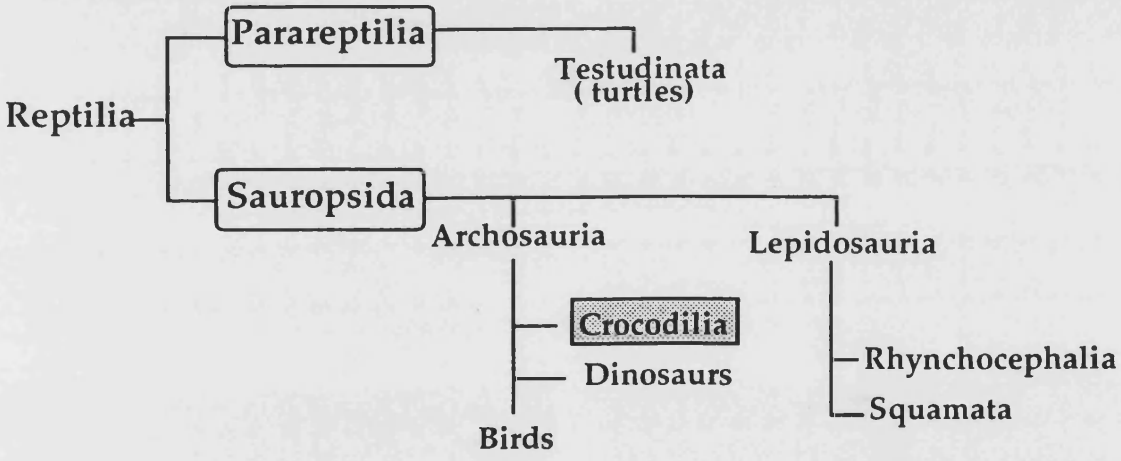
II - ANATOMY OF THE NECK REGION

CHAPTER (2)

CROCODILIA

{ One example from group Crocodilia (Family Alligatoridae, e.g.*Caiman crocodilus*) was dissected and used as a comparision to group Lepidosauria (Rhynchocephalia and Squamata), therefore it was located first as chapter 2}.

Crocodilians are the only living reptilians belonging to the group Archosauria (Densmore and Owen, 1989). With birds, they represent the only living relatives of extinct dinosaurs and form the living sister taxon of Lepidosauria. Colbert and Mook (1951), Walker (1970), Whetstone and Whybrow (1983), thought that the earliest crocodilians were probably terrestrial in habit, although living ones are adapted for living in and around the water. The earliest fossil crocodiles are found in Triassic rocks (Steel, 1973; Tarsitano et al, 1989).



Crocodiles are differentiated from other living reptiles by specialisations such as: head elongated with thick skin fused to bone; nostrils and ears close under water with watertight valves, and the nostrils are located on the tip of the snout (to help the animal breathe at the surface while the rest of the body is submerged); a powerful blade-like tail which is equal

or longer than the body, and used in swimming and defence; body covered with thick, non-overlapping scales underlain by osteoderms; teeth embedded in sockets; and a tongue with a flap that attaches to the hind end of the mouth to shut off the respiratory passage during diving (Magnusson, 1993). Crocodiles are the major freshwater predators of the tropics and subtropics (only 3 species extend to the temperate zone). They include 3 families, 8 genera and about 23 species which inhabit Africa; Central, North and South America, Asia and Australia.
Owen (1866), Mook (1934), Wermuth (1953), and Steel (1973) subdivided the recent Crocodilia into 3 groups (Frey et al., 1989):

Family: Alligatoridae (dissected specimen)

Alligators rang from 2 - 4 m length, and inhabit tropical North and South America, and warm temperate subtropical China. They are divided into two subfamilies: the alligators e.g. *Alligator mississippiensis* and the caimans e.g. the South American *Caiman crocodilus* .

Family: Crocodylidae

These include freshwater and nearshore-marine forms that occur worldwide in tropical areas such as Africa, Madagascar, Asia, East Indies, Australia, Central America, North and South America. They range in length from 1.5 - 7.5 m. There are two subfamilies: the Crocodylinae (e.g. the American salt water *Crocodylus acutus*), and the Tomistominae (e.g. *Tomistoma schlegeli*).

Family: Gavialidae

These are fresh water reptiles found in lakes, swamps and rivers. The length ranges from 3 - 6.6 m, and they are found in Thailand, Malaysia and the islands of Sumatra, Borneo, Java and possibly Sulawesi.
Gavials are characterised by their extremely long, slender snout which is considered to be an adaptation for fish eating. They spend more time in

water than other crocodilians. A typical example is *Gavialis gangeticus* which is around 6.5 m. length (Zug, 1993; Magnusson, 1993).

Anatomy of the neck region in Crocodilia

Family Alligatoridae

Caiman crocodilus Dissected specimen

Crocodylus niloticus. Skeletal specimen

Alligator mississipensis " "

Previous work:

Mook, 1921; Goodrich, 1930; Wermuth, 1953; Hoffstetter and Gasc, 1969; Iordansky, 1964, 1973; Seidel, 1978.

Osteology of *Caiman crocodilus*

(Plate 2.1)

Skull

Note: The mid-posterodorsal part (parietal/oto-occipital region) of the skull was already destroyed in the dissected specimen due to a dissection of the brain.

1- Parietal

This wide rectangular plate has a smooth mid-posterodorsal margin (where depressor mandibulae externus originates). It was hard to observe any fenestra between the occipital and the parietal, although Iordansky (1973) observed a narrow slit, the post-temporal fenestra. Posterolateral parietal processes are absent (plate 2.1a) (Wermuth, 1953).

2- Squamosal

This has a rectangular shape (quadriradiate) with a lateral expansion toward the quadrate (plate 2.1a) (where the depressor mandibulae internus originates). It meets the paroccipital process and the supraoccipital laterally. The squamosal expands dorsally and laterally,

but does not reach the mid-dorsal line. Dorsally, the supratemporal fenestrae are located between parietal and squamosal (Iordansky, 1973).

3- Supratemporal

Absent (Iordansky, 1973).

4- Quadrate

This is a wide inclined bone that is fused to the braincase and the quadratojugual ventrally. The bone contacts the squamosal dorsally (where depressor mandibulae internus originates), and is sutured to the quadrojugual ventrally (with the jugal they form the lower temporal arch and border the lateral temporal fenestra) (plate 2.1a) (Iordansky, 1973).

5- Retroarticular process

This well-developed process bears a strong posterodorsal curvature (where depressor mandibulae internus and externus insert) (Iordansky, 1973).

6- Supraoccipital

Superiorly, it has a rounded midline ridge (where rectus capitis inserts). Superficial to the supraoccipital, Mook (1921) described a separate ossification called processus postoccipitales.

7- Oto-occipital

The paroccipital process is narrow (where obliquus capitis, longissimus capitis 2 and longus colli lateralis insert).

8- Paroccipital epiphysis

Absent.

9- Basioccipital

The basal tubera have elongated narrow epiphyses which extend ventrally and laterally. The bone possesses a deep median crest which separates the basal tubera and is bounded by a shallow concavity on both sides (where longissimus capitis 4 inserts). According to Hoffstetter and

Gasc (1969) the occipital condyle in crocodilians is formed by the basioccipital alone.

Presacral vertebral column

1- Atlas

The atlantal neural arch has a short posterior process and Goodrich (1930) and Hoffstetter and Gasc (1969) recorded the presence of an anterior proatlas. Ventrally, the atlas intercentrum give attachment with a wide lateral rib (first cervical rib) (plate 2.1b).

2- Axis

The postzygapophyses are smooth and inclined (45°), and the transverse processes are weak. The second ventral process (~ intercentrum) is keeled but shallow, while the third ventral process (~ intercentrum) is deeply keeled, and is fused to the centrum behind (C3) (Hoffstetter and Gasc, 1969). The second bicipital rib is attached to the atlantal centrum which is fused to the axis.

3- C3-9

There are 9 cervical vertebrae and 12 ventral processes (~ intercentra [1 flat + 11 keeled] end on D4) (Hoffstetter and Gasc, 1969). The height of the neural spines is similar throughout. Their tips are compressed and the dorsal ends are short. The anterior margins of the spines are smooth and curved (anteriorly), while the posterior margins are smooth and straight. The neural spines become narrow and vertical posteriorly (after C3). The postzygapophyses are smooth and inclined. Overall, the cervical region has a dorsal cyrvature (Seidell, 1978) (Fig. 2.1). The centra are procoelous (Hoffstetter and Gasc, 1969), and their width is greater than their length. The postzygapophyses are smooth and inclined. Ventrally, there are no mid-ventral keels between ventral processes
(~ intercentra) which are smooth and fused to the centrum behind (Hoffstetter and Gasc, 1969).

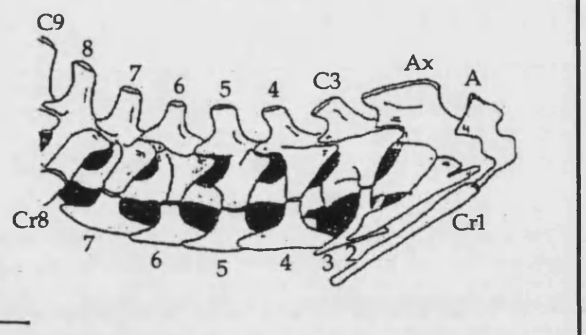


Fig. (2.1) Right lateral view of the cervical vertebrae showing the various shapes of the ribs in *Caiman crocodilus*. Scale bar = 1 mm.

3- Anterior trunk vertebrae (dorsal)

The neural spines are long and wide with elongated compressed tips. The anterior and posterior margins of the spines are smooth and straight. Ventrally, the keeled intercentra continue along D1-3 and this may be related to the longus colli attachments (Hoffstetter and Gasc, 1969).

Ribs

The first cervical rib is flat and single-headed (Hoffstetter and Gasc, 1969) and articulates with the first intercentrum. It extends laterally and has a pointed distal end. The second cervical rib is bicipital and articulates with the atlantal centrum of the atlas which is fused to the axis (no rib attaches to the axis transverse process). It has a long pointed distal end. Hoffstetter and Gasc (1969) stated that both first and second ribs were able to slide anteriorly, and the distal end of the ribs were bounded by fibrous tissue. The third to seventh ribs are very short with a transverse shaft (anterior and posterior crests), and are also bicipital (well developed capitulum and tuberculum with a strongly projecting parapophysis and diapophyses on the centra) (Hoffstetter and Gasc, 1969). The eighth and ninth ribs (last cervical) + tenth to eleventh ribs (anterior dorsal) are long and bicipital (Fig. 2.2). From vertebra 12 onwards, the ribs are long and have a single head (synapophysis) with a cartilaginous uncinate processes (Hoffstetter and Gasc, 1969). Rib ligaments are absent.

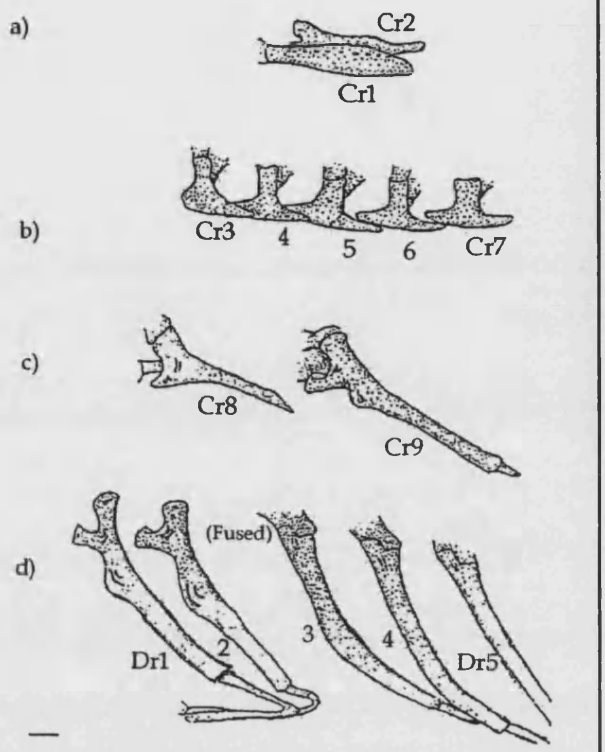


Fig. (2.2) Left lateral view of the rib region, a) cervical ribs (Cr1-2); b) cervical ribs (Cr3-7), short shafts, bicipital; c) last cervical ribs (Cr8-9); d) dorsal ribs (Dr1-2), bicipital, and dorsal ribs (Dr3-5) unicipital in *Caiman niloticus*. Scale bar = 1 mm.

Pectoral girdle

1- Sternum

Well developed.

2- Interclavicle

It is a long rod-shaped bone that extends above the sternum ventrally (plate 2.1d).

3- Clavicle

Absent

4- Scapulocoracoid and suprascapula

The coracoid is a solid bone that attaches to wide elongated wide scapula. The suprascapula arises dorsally from the scapulocoracoid as a small crest (plate 2.1c).

Muscles of *Caiman crocodilus*

Note: In this and all subsequent chapters there are some muscles that either do not vary significantly from the general morphology described in chapter 1, or were not investigated to any degree (e.g. deep spinalis muscles). In these cases, the reader is always referred back to chapter 1 for the general description.

(Plate 2.2)

Superficial muscles

1- Depressor mandibulae internus and externus

The depressor mandibulae internus originates from the modified quadrate and the large squamosal. Iordansky (1964) referred to the squamosal as an important area for the origin of mandibular adductor muscles. The externus branch originates from the parietal. The muscles insert in series on the retroarticular process (Iordansky, 1973).

2- Cervicomandibularis

See chapter 2 (arises most probably from the muscle fascia of longissimus capitis 1).

3- Trapezius

Originates from the mid-dorsal line (spine tips), and inserts on the anteroventral surface of the scapula.

4- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the anterior margin of the sternum (plate 2.2a), and inserts on the distal end of the atlas rib and the muscle fascia of longus colli (plate 2.2c).

2- Levator scapula dorsalis and ventralis

Both muscles originate from the distal end of the first cervical rib (atlas), and insert on the anterior margin of the scapulocoracoid and towards the lower side of the suprascapula.

3- Clavicle dorsalis

Absent.

4- Ribs to suprascapula / scapula muscle slips

The suprascapula gives attachment to an anterior muscle that arises from the muscle fascia of the longissimus dorsi. Dorsally and internally the suprascapula gives attachment to a number of muscles that arise laterally from the C7-D1 ribs. Posteriorly the suprascapula also gives attachment to a flat muscle that extends from its origin on the D2 rib, while a further wide muscle slip runs from the D3-4 rib to the posterior edge of the scapula (plate 2.2b).

Deep muscles

1- Obliquus capitis

Originates from the C2-8 neural spines, and extends anteriorly in one flat layer to insert on the dorsal side of the paroccipital process.

2- Rectus capitis

Originates from C1 neural arch, and inserts on the supraoccipital.

3- Splenius capitis

Originates from C3-9 neural spines and muscle fascia of longissimus dorsi, and extends anteriorly as a single trunk above the cervical spines to insert on the mid-posterodorsal margin of the parietal.

4- Spinalis muscles

a) Spinalis capitis

Absent.

b) Spinalis / Semispinalis cervicus and Spinalis / Semispinalis complex

Not investigated during dissection.

5- Longissimus muscles

a) Longissimus capitis 1

Absent, and instead the depressor mandibulae externus originates from the parietal.

b) Longissimus capitis 2

Branches along the anterior cervical vertebrae and extends anteriorly to insert on the lateral side of the paroccipital process.

c) Longissimus capitis 3

Absent.

d) Longissimus capitis 4

Runs deeply and ventrally under longissimus capitis 2. The muscle inserts on the shallow concave area of the basioccipital deep to the longus colli centralis attachment and anterior to the occipital condyle (plate 2.2d). Iordansky (1973) called it "M. occipitotransversalis profundus".

e) Longissimus capitis minor

Absent.

g) Longissimus cervicus

See chapter 1.

6- Iliocostalis muscles

a) Iliocostalis major

See chapter 1.

b) Iliocostalis cervicus

Extends anteriorly to insert on the muscle fascia of the longus colli and on the atlas rib (plate 2.2c).

7- Longus muscles

a) Longus colli centralis and lateralis

The longus colli lateralis originates from the D5 centrum (tendon), by slips from the ventral processes, centra and inner section of the bicipital ribs of C5-D3, and from C2-7 short ribs to insert broadly on the posteroventral side of the paroccipital process (plate 2.2c). The longus

colli centralis ("M. basioccipito vertebralis"- Iordansky, 1973) originates from the apices of the second to sixth ventral processes apices (intercentra) and extends anteriorly and centrally to insert on the curved longitudinal epiphyses of the basal tubera (superficial to the longissimus capitis 4 insertion).

(Fig. 2.3)

B) Longus cervicus

Absent.

8- First flat intercentral muscle slip to basioccipital

Ventrally, the first ventral process muscle (~ intercentrum) inserts on the basal tubera partially superficial to the longus colli centralis insertion.

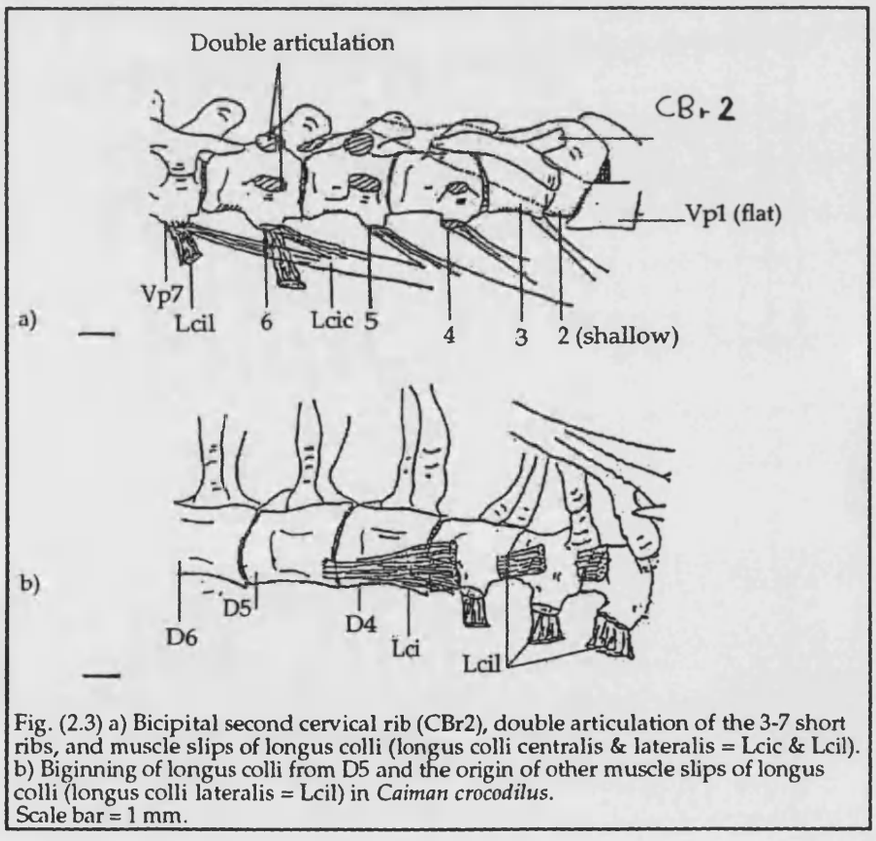


Fig. (2.3) a) Bicipital second cervical rib (CBr2), double articulation of the 3-7 short ribs, and muscle slips of longus colli (longus colli centralis & lateralis = Lcic & Lcil). b) Biginning of longus colli from D5 and the origin of other muscle slips of longus colli (longus colli lateralis = Lcil) in *Caiman crocodilus*.
Scale bar = 1 mm.

9- Posterior intercentral muscle slips to skull

Absent.

Very deep muscles

1- Deep oblique intercentral muscle slips to rib

Short oblique muscle slips that connect the anterior ventral processes to the ribs such that:-

Second ventral process (intercentrum) (C2, axis).....connects to C1-2 ribs.

Third " " (C3) .....connects to C3-4 ribs.

Fourth " " (C4) .....connects to C4-5 ribs.

Fifth " " (C5) .....connects to C5-6 ribs

Special craniocervical anatomical features in *Caiman crocodilus*

Osteology

Skull

1- The posterolateral processes of the parietal are absent.

2- The squamosal is quadriradiate.

3- The supratemporal is absent.

4- The quadrate is immovable and sutured to the quadratojugal.

5- The basioccipital has a deep median crest that separates the basal tubera.

Presacral vertebral column

1- The atlas has a flat intercentrum, and bears the first cervical rib.

2- There are 9 cervical vertebrae, 1 flat intercentrum and 10 keeled intercentra.

3- The anterior dorsal vertebrae have keeled intercentra.

Ribs

1- The 2nd-11th ribs are bicipital, the 2nd and 8th ribs have long shafts while the 3rd - 7th ribs have horizontal anterior and posterior crests with a well-developed capitulum and tuberculum. The 1st, 12th and posterior ribs are unicipital.

2- Rib ligaments are absent.

Pectoral girdle

1- The interclavicle is rod-shaped.

2- The clavicle is absent.

Myology

Superficial muscles

1- The depressor mandibulae externus originates from the parietal only, and inserts on the retroarticular process in series.

2- The trapezius inserts on the scapula.

Intermediate muscles

1- The episternocleidomastoid originates from the sternum in the absence of the clavicle, and inserts on the C1 rib.

2- The levator scapula dorsalis and ventralis insert on the C1 rib.

3- The clavicle dorsalis is absent.

4- Deep rib to suprascapula muscle slips are absent.

Deep muscles

1- The obliquus capitis originates from C2-8 neural spines.

2- The splenius capitis originates from C2-9 neural spines and muscle fascia.

3- The longissimus capitis 1, 3 and minor are absent.

4- The iliocostalis cervicus inserts on the atlas rib and muscle fascia of longus colli.

5- The longissimus capitis 4 inserts broadly on the basioccipital deep to longus colli.

6- The longus colli is divided into two parts, a central branch that originates from the 2nd-6th intercentra and inserts on the basioccipital, and a lateral branch that originates from the D5 centrum and inserts laterally on the paroccipital process.

7- Longus cervicus is absent.

8- The posterior intercentral muscle slips to skull are absent.

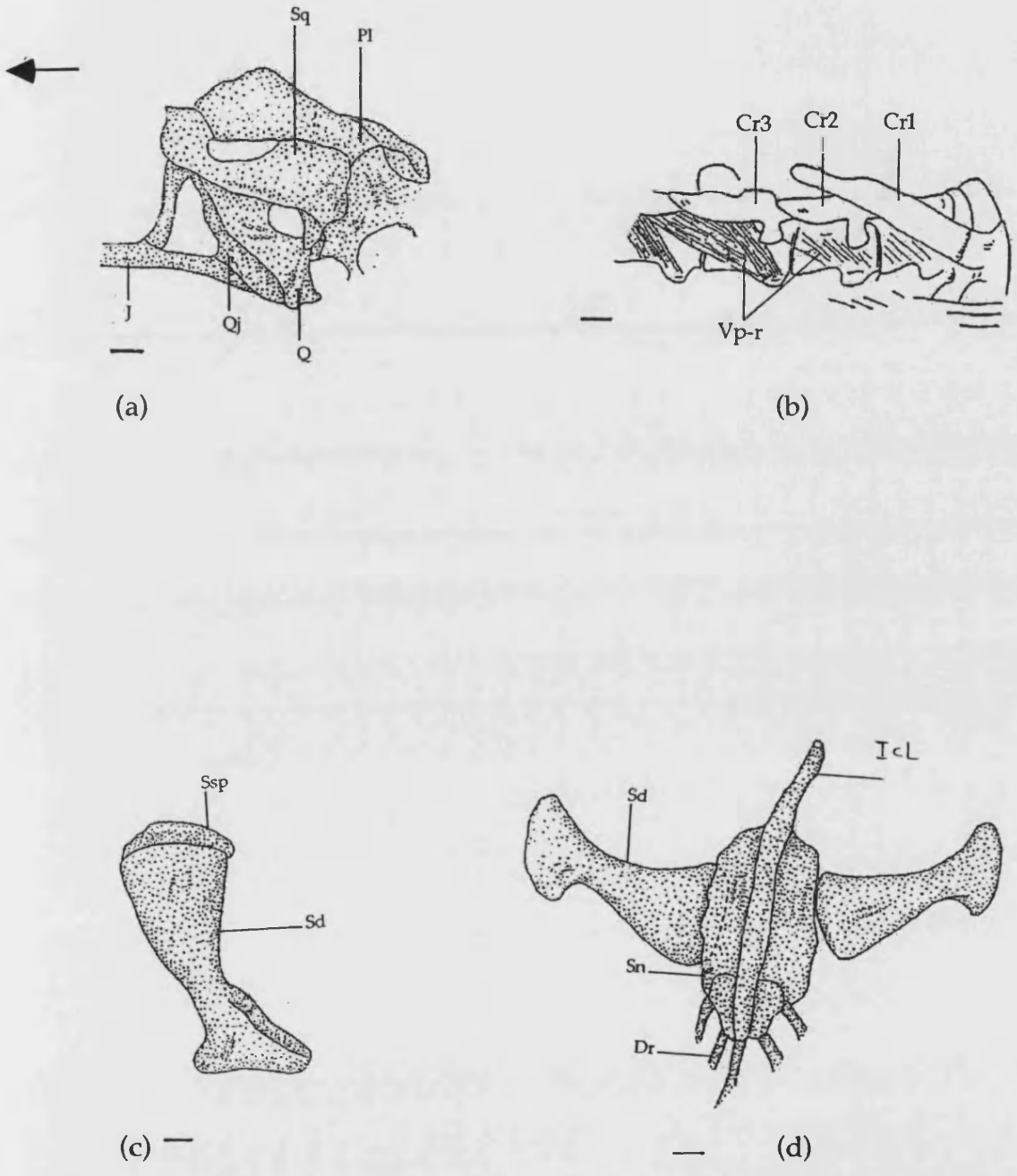


Plate (2.1) *Crocodylus niloticus*, a) left posterolateral view of the skull with wide squamosal (Sq) and fixed quadrate (Q); b) very deep central muscles, and the first axis rib where some deep muscle insert; c) right lateral view of the pectoral girdle showing the suprascapula (Ssp) and scapulocoracoid (Sd); d) ventral view of the pectoral girdle showing the rod-shaped interclavicle (Icl), sternum (Sn) and scapulocoracoid (Sd). Scale bar = 1 mm.

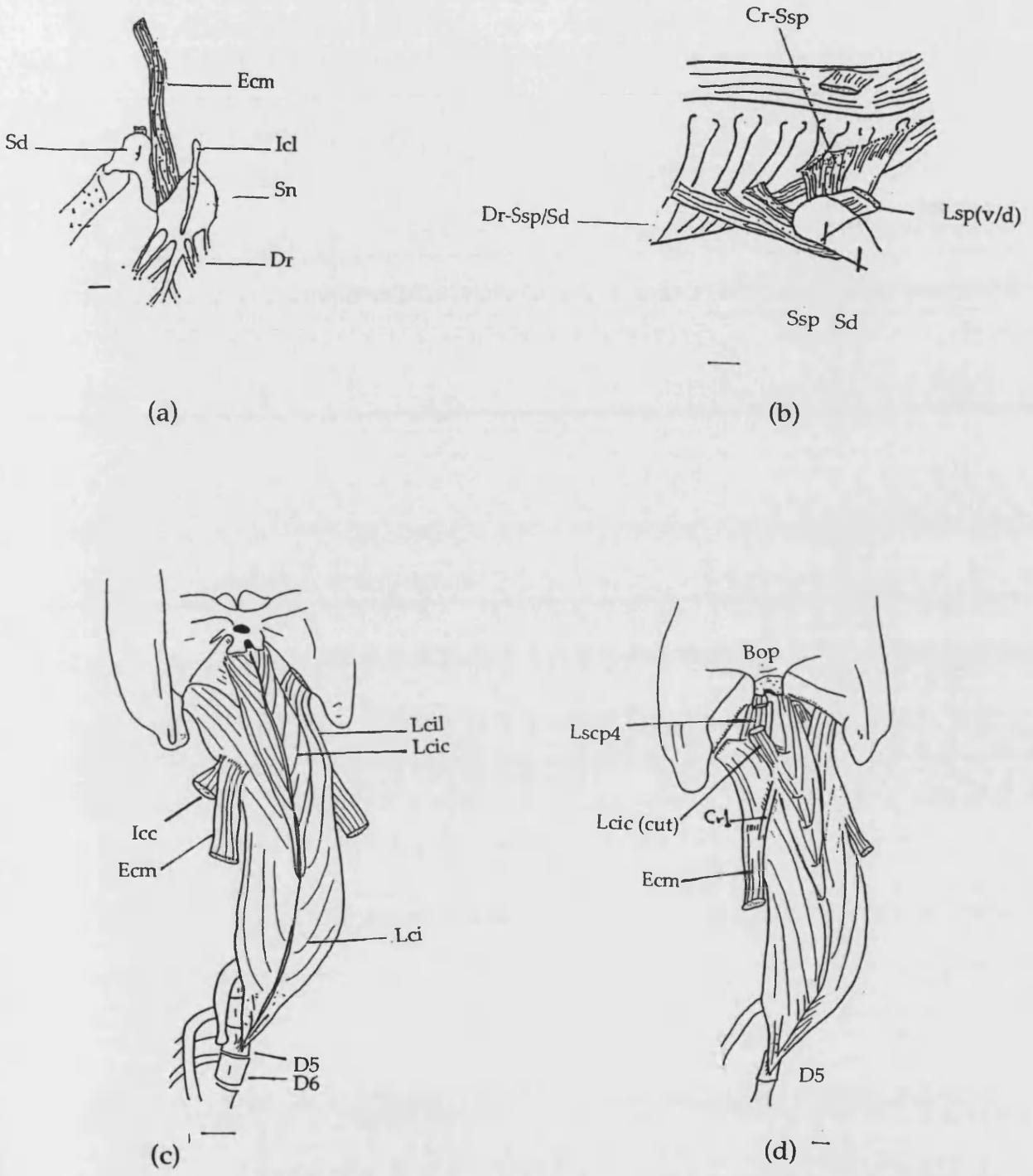


Plate (2.2) *Caiman crocodilus*, a) ventral view of the pectoral girdle showing the origin of episternocleidomastoid (Ecm) from sternum (Sn); b) right lateral view of the pectoral girdle region showing the cervical rib to suprascapula muscle slips (Cr-Ssp) and dorsal rib to suprascapula & scapulocoracoid muscle slips (Dr-Ssp/Sd); c-d) division of longus colli (Lci) during insertion on basioccipital and paroccipital process (Lcic & Lcil), iliocostalis cervicus (Icc) and episternocleidomastoid (Ecm) insertion on the atlas rib (Cr1), and origin of longus colli (Lci) from D5. Scale bar = 1 mm.

CHAPTER (3)

SPHENODON PUNCTATUS

Life history:

The genus *Sphenodon* of New Zealand is the sole survivor of the flourishing and widespread Mesozoic group Rhynchocephalia, it is represented by two species *S. punctatus* and *S. guntheri*. The group originated from small terrestrial diapsids during the Permo-Triassic period. Nevertheless, the first member of this group is recorded from the Late Triassic (Evans, 1988). During the Triassic and Jurassic periods the "beak head" rhynchocephalians were abundant, and fossils are known from North America, Europe, Asia and Africa (Whiteside, 1986; Fraser, 1988). Recent studies show that *Gephyrosaurus* and sphenodontians form the group Rhynchocephalia and together with the Squamata (lizards, snakes and amphisbaenians) constitute the Lepidosauria (Gauthier, 1988).

Recent location:

Sphenodon is now extinct on the New Zealand mainland (Cree and Daugherty, 1990), but survives on about 30 small offshore islands in Cook Strait and off the North - East coast of North Island (Newman, 1987). The largest population of Tuataras (*S. punctatus*), with remarkable diversity, were found in Takaporewa in Stephens Island (Daugherty, 1990).

Lifestyle:

The Tuatara lives in cold damp surroundings that are perfect for its low body temperature. Tuatara live in burrows made by Toral birds and feed on invertebrates, such as cricket - like insects called wetas and small vertebrates (e.g. lizards; frogs and small tuataras). Fossil sphenodontians generally appear to have lived a similar lifestyle to their modern descendants, although some (*Pleurosaurus*) were aquatic.

Anatomy of the neck region in *Sphenodon punctatus*

Group: Rhynchocephalia

Family: Sphenodontidae

Genus : *Sphenodon.*

Sphenodon punctatus – Tuatara = Dissected specimen.

Previous works:

Albrecht, 1883; Howes and Swinnerton, 1901; Hoffstetter and Gasc, 1969.

Osteology of *Sphenodon*

(Plate 3.1 - 3.2)

Skull

1- Parietal

Dorsally (plate 3.1b), this bone is T-shaped with short posterolateral processes (where depressor mandibulae originates and longissimus capitis 1 attaches); ventrally it meets the supraoccipital, anteriorly it is sutured to the frontal, and laterally it forms the inner borders of the upper temporal fenestrae.

2- Squamosal

In lateral view (plate 3.1a), this is large and quadriradiate; dorsally it meets the parietal; ventrally the quadrate; posteriorly the back of the paroccipital process; and anteriorly the postorbital, forming the upper temporal bar. The squamosal surface is roughened with pits and ridges (where depressor mandibulae originates). Both squamosal and parietal border the upper temporal opening in conjunction with the post-frontal and postorbital (Broom, 1925).

3- Supratemporal

Is absent in the adult, but is fused to the squamosal in hatchlings (Broom, 1925).

4- Quadrate

Laterally (plate 3.1c), this bone is triradiate with a medial cavity and a wide ventral articular condyle. Anterodorsally, it contacts the squamosal; anteroventrally, the quadratojugal (Broom, 1925); and ventrally, the articular. The quadrate is immovable (Whiteside, 1986; Fraser, 1988).

5- Retroarticular process

Laterally (plate 3.1c), the process is reduced and has some ridges and elevations (the depressor mandibulae internus attaches on the small depression internally, while the depressor mandibulae externus attaches on the external bony extension).

6- Supraoccipital

Posteriorly, the lateral margin of the supraoccipital has a shallow ridge (where rectus capitis inserts), and it possesses a posterior crest (plate 3.1d) (where the axis to supraoccipital muscle inserts).

7-Oto-occipital

In *Sphenodon*, unlike lizards, the opisthotic is not fused to the exoccipital. The lateral part of the opisthotic is extended into a narrow paroccipital process, with longitudinal striae (where the lateral branch of the episternocleidomastoid inserts). The exoccipital meets the supraoccipital with a small crest (where the proatlas tendinous fibres insert), and meets the basioccipital ventrally along a smooth edge.

8- Paroccipital epiphysis

Absent.

9- Basioccipital

The basal tuberculum is triangular and bears two epiphyses (the medial epiphysis where longus colli inserts, and the lateral epiphysis where longissimus capitis 4 inserts).

Presacral vertebral column

1- Proatlas

This tiny bone (where longissimus cervicus anterior attaches) is connected to the skull by a ligament which inserts on a bony crest between the supraoccipital and exoccipital (plate 3.4c) (Albrecht, 1883; Hoffstetter and Gasc, 1969).

2- Atlas

The lateral side of each atlantal arch retains a long posterior process that is directed up wards (plate 3.2a) (where the longissimus cervicus posterior inserts). The transverse process lacks a posterior projection and instead bears a small bony elevation (where the levator scapula ventralis and dorsalis originate). The atlas centrum possesses a small ridge above the transverse process (where iliocostalis cervicus inserts). The intercentrum is flat with a shallow depression (where the first intercentral muscle to basioccipital originates).

3- Axis

The neural arch has a keeled dorsal end (where the axis to supraoccipital muscle originates), and a triangular posterodorsal process (where the anterior splenius capitis and spinalis cervicus muscle slips originate). The horizontal postzygapophysis possesses a tubercle with a small posterodorsal crest (where the spinalis cervicus inserts). The long axis of the centrum has a dorsolateral crest (plate 3.2b) (where longissimus capitis 3 originates), and a ventrolateral process, which projects strongly posteriorly (where the iliocostalis major attaches). Ventrally, the second intercentrum is flat. It has two lateral prolongations (where the V-shaped longus cervicus inserts). The posterior margin of the axis centrum is partially covered by the

first sutured keeled intercentrum (where the single posterior intercentral muscle to basioccipital originates).

4- C3-8

There are 8 cervical vertebrae in the living genus (Howes and Swinnerton, 1901; Osborn, 1903), but Jurassic rhynchocephalians are recorded with 7 cervical vertebrae (Hoffstetter and Gasc, 1969). The neural spines of the cervical vertebrae are long, with a wavy posterior edge that becomes less obvious towards C8 (where the spinalis\semispinalis cervicus + splenius capitis deep slips attached). The height of the spine starts to increase around

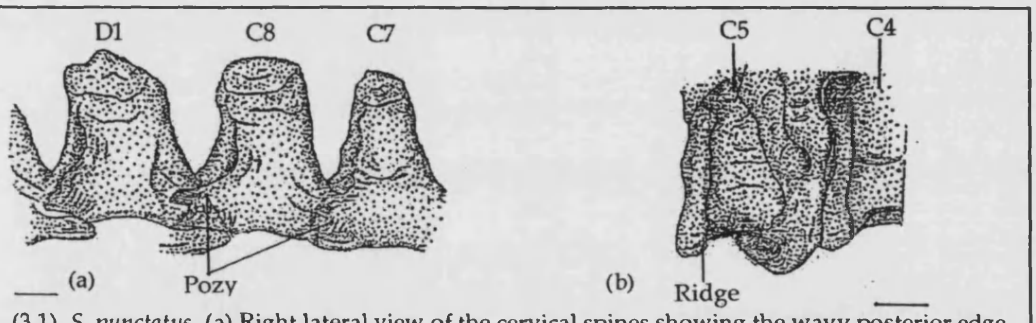


Fig. (3.1), *S. punctatus*, (a) Right lateral view of the cervical spines showing the wavy posterior edge of the spines, the posterior processes of the postzygapophyses (Pozy). b) Right ventrolateral view of the cervical centra showing the ventral midline keel or ridge of C4 & 5. Scale bar = 1mm.

The anterior edges of the cervical and dorsal spines possess small tips (where the splenius capitis muscle slips originate). The angle of the articular surfaces of the zygapophyses of C8 + D1 increases to about 60° from horizontal. The centra are amphicoelous (Osborn, 1903). The postzygapophyses have posterior processes (where the splenius cervicus and spinalis semispinalis muscles attach) (Fig., 3.1).

Ventrally, the cervical vertebrae retain two flat intercentra, followed by seven keeled intercentra with a small ventral keel (Diagram 3.1). The keeled intercentra are shallow with a plain round end. The keel gets weaker towards the end of the cervical region (the last deep intercentrum is between C8 and D1), then simple U-shaped intercentra are retained through

the presacral, sacral and caudal regions. This condition is found also in the extinct *Gephyrosaurus* (Evans, 1981).

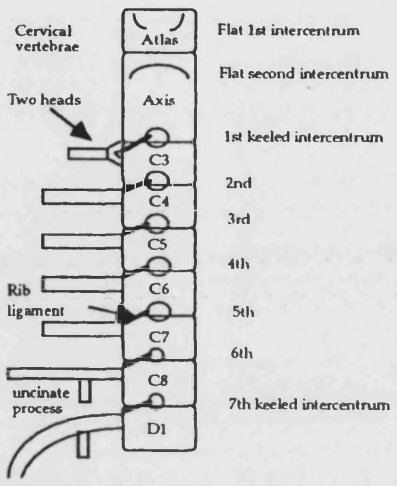


Diagram (3.1) of the ventral side of the cervical vertebrae in *S. punctatus*.

The centra possess a ventral midline keel from C3 - D1, while the following vertebrae have a more rounded to flat surface (the keel is associated with the deep longus colli and cervicus muscles). The second intercentrum is flat but has lateral crests. The third intercentrum " first keeled intercentrum" has two lateral bony extensions for the deep longus cervicus tendon. The fourth to sixth keeled intercentra have lateral and basal crests Fig. (3.2). The longus cervicus muscle slips attach to the lateral crests, while the basal crests bear attachment regions for posterior rib ligaments joining the intercentra and transverse processes/ribs. The 8th and 9th intercentra are roughened with depressions (where the longus colli originates).

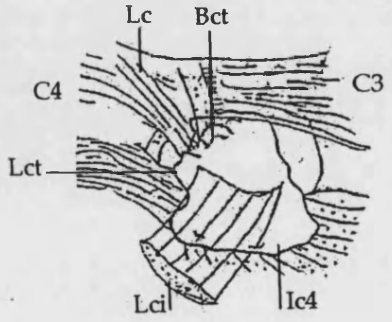


Fig. (3.2) *S. punctatus*, right ventrolateral view of C3 & 4 showing the 4th intercentrum (Ic4) with basal & lateral crests (Bct & Lct). Longus colli = Lci; Longus cervicus = Lc. Scale bar = 1 mm.

5- Anterior dorsal vertebrae (D1, D2, ...etc)

The splenius capitis tendon originates from the anterior tips of D4-1, where the neural spine possesses a tiny anterior tubercle for muscle insertion. The neural spines of the dorsal vertebrae become higher and wider than those of cervical region, with smooth curved anterior and posterior margins.

6- Ribs

Rib ratio = 2 + 1 + 4 +1 (plate 3.5b) (Osborn, 1903; Hoffstetter and Gasc 1969). The first rib is on C3. It is short and articulates with two lateral facets on C3 (bicipital head) (Hoffstetter and Gasc, 1969). The distal end is pointed. The 2nd-6th free ribs are longer with a cartilaginous distal end. Ventrally, the presacral ribs connect to the intercentra by a connective tissue band. The 1st rib to attach to the sternum is that of D1, where the trunk region starts. The trunk ribs are long and thin with a cartilaginous ventral section. The proximal part of the ribs (beginning from C8) bears an uncinate process, and this feature is found throughout the presacral region (plate 3.2c, 3.3d) (Hoffstetter and Gasc, 1969).

Pectoral girdle

1- Sternum

The cartilaginous distal end of the D1-3 ribs attach to the flat sternum (sternal ribs), while the rest do not (post-sternal ribs). Posteriorly, the sternum meets the gastralia ventrally where the sub-iliocostalis muscle slips attach.

2, 3, 4- Clavicle, interclavicle, scapulocoracoid

The pectoral girdle in *Sphenodon* resembles that of the extinct *Gephyrosaurus bridensis* (Evans, 1981). The non-fenestrated coracoid lies anterior to the sternum and meets the elongated curved scapula dorsally. The scapula is extended dorsally by the non-ossified suprascapula. The suprascapula

overlaps vertebrae 6 - 9 dorsally and is pointed posteriorly (where the levator scapula dorsalis muscle originates). Anteroventral to the coracoid is the T-shaped interclavicle (Osborn, 1903). It has two long narrow, lateral arms (where episternocleidomastoid originates) and a long posterior stem; Bellairs (1969) described it as a dagger - shaped or cruciform. The solid clavicle attaches dorsally to the scapula by its acromial end.

Muscles of *Sphenodon*

(Plate 3.3 - 3.4 - 3.5)

Superficial muscles

1-Depressor mandibulae

Depressor mandibulae internus and externus originate from the skull roof (parietal + squamosal) (plate 3.3a), and insert on the retroarticular process (overlapping each other). The wide muscle leaves depressions on the articular and roughened surfaces on the squamosal and parietal.

2- Cervicomandibularis

Originates dorsally from the fatty tissue and muscle fascia of splenius capitis, and inserts on the retroarticular process. The muscle overlaps C1-2 spines.

3- Constrictor colli

See chapter 1.

4- Trapezius

Originates from the fatty tissue and muscle fascia dorsally, but does not extend to the mid-dorsal line, and inserts on the anterior dorsal edge of the clavicle.

5- Latissimus dorsi

See chapter 1.

6- Sub-iliocostalis rib muscle slips (uncinate processes muscle slips)

Run superficially above the iliocostalis major slips. Each slip attaches to the uncinate processes of the trunk rib and extends posteroventrally to insert on the gastralia (plate 3.3e).

Intermediate muscles

1- Episternocleidomastoid

Originates ventrally from the clavicle and interclavicle, and runs obliquely and anteriorly to insert on the dorsal skull roof (parietal + squamosal) and paroccipital process (plate 3.4a) such that:

Branch 1..... inserts on the external lateral end of the paroccipital process.

Branch 2 ..... inserts above branch 1 on the medial side of the squamosal close to the paroccipital process.

Branch 3 ..... inserts directly below the depressor mandibulae on the dorsal part of the squamosal and the adjacent parietal.

2- Clavicle dorsalis

Originates from the clavicle laterally, and inserts on the central part of the parietal and the muscle fascia dorsally. The whole muscle runs obliquely below the constrictor colli and cervicomandibularis and runs anteriorly parallel to the trapezius.

3- Levator scapula dorsalis and ventralis

Both muscles originate from the atlas transverse process, and insert on the suprascapula (levator scapula dorsalis), and on the anterior edge of the scapula above the clavicle, where the trapezius attaches (levator scapula ventralis).

4- Ribs to suprascapula/scapula muscle slips

The suprascapula/scapula muscles originate from the cartilaginous distal end of the cervical ribs and first trunk rib. The superficial suprascapula muscle slips insert on the anterior, dorsal and posterior margins of the suprascapula. Their anterior slips originate from the first and second cervical ribs, the dorsal slips originate from the third, fourth and fifth cervical ribs, and the posterior slip originates from the sixth cervical rib and first trunk rib (plate 3.3c). The first trunk rib muscle also inserts on the posterior margin of the scapula. The deep suprascapula muscle slips originate from the fourth and fifth cervical ribs (wide cartilaginous ends are present).

Deep muscles

1- Rectus and obliquus capitis

The rectus capitis originates from the atlantal arch and the anterodorsal part of the axis, and inserts on the supraoccipital. The obliquus capitis originates from the axis neural arch, and extends as one flat muscle bundle to insert on the paroccipital process close to its suture with the supraoccipital.

2- Axis to supraoccipital

Originates from the axis mid-dorsal margin, and inserts on the supraoccipital dorsal crest (plate 3.4a).

3- Splenius capitis and cervicus

Originates posteriorly and superficially (tendinous bundles) from C6 –D4 neural spine tips, and anteriorly deep (muscle fibers ~ splenius cervicus) from C2-8 neural spine posterior margins (= wavy posterodorsal edge of the cervical spines). The muscle extends forward to insert on the parietal.

4- Spinalis and semispinalis muscles

a) Spinalis/semispinalis cervicus

Both muscles interconnect along D4 to form a tendinous sheet where the cervicus bundle originates. It runs anteriorly and inserts as a series of muscle slips on C2-7 neural arches and postzygapophyses (small tubercles and depressions for muscle attachment).

b) Deep spinalis \semispinalis complex

See chapter 1.

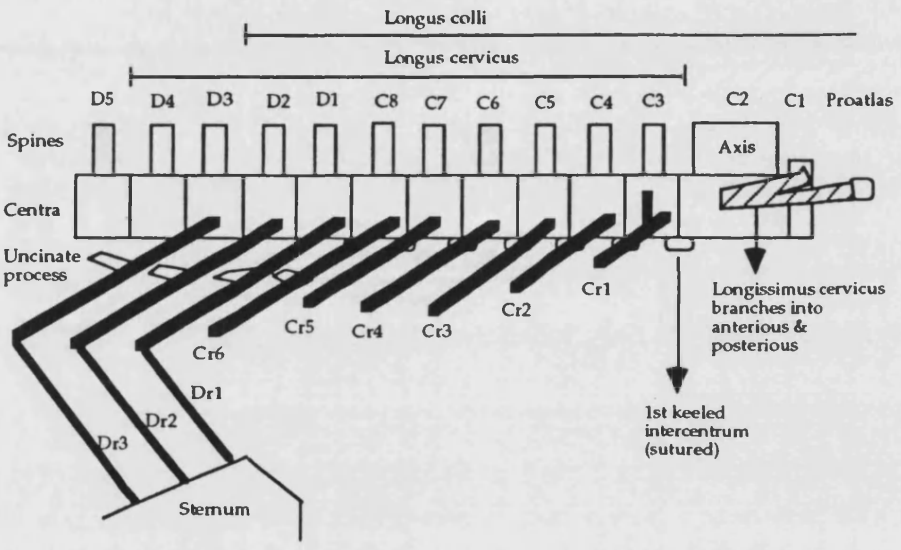


Diagram (3.2) *S. punctatus,* right lateral view of cervical and dorsal vertebrae.

5- Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus cervicus anterior and posterior

It branches from longissimus dorsi, and inserts on the atlas posterior process (posterior) and proatlas (anterior).

c) Longissimus capitis 1

Branches from the longissimus dorsi along C7, and extends anteriorly to insert on the parietal and squamosal.

d) Longissimus capitis 2

Branches from the longissimus dorsi along C3, and inserts anteriorly on the paroccipital process.

e) Longissimus capitis 3

Branches from the longissimus dorsi along the anterior prezygapophyses, and inserts on the ventral edge of the paroccipital process near the exoccipital. The muscle branches beside a small lateral bony crest (process) on the axis centrum above the axis transverse process (plate 3.2b).

f) Longissimus capitis 4

Branches laterally from the longissimus dorsi along C2, and inserts ventrally on the dorsolateral tips of the basal tubera. The muscle attaches to one of the lateral tuberal epiphyses.

g) Longissimus capitis minor

Absent.

6- Iliocostalis muscles

a) Iliocostalis major

See chapter 1.

b) Iliocostalis cervicus

Branches from the iliocostalis major along C2, and inserts on the ventral side of the atlantal arch towards the levator scapula dorsalis and ventralis origin.

7- Longus muscles

a) Longus colli (superficial, intermediate, and deep sections)

Generally, the muscle originates from the 11th intercentrum (between D2-3) and C8 rib, and is divided into three sections (plate 3.5a): the first superficial section originates from intercentrum 8 (= 6 keeled intercentrum apex) between C7-8, and runs deep to join the second section. The second intermediate section starts from the flat intercentrum 10 between D1-2, and

runs ventrolaterally deep to the previous section originating from the anterior rib ligaments and centra. The third lateral section begins from the flat intercentrum 11 between D2-3 and from C8 rib (6th cervical rib), and extends laterally by joining the previous two sections (plate 3.5c). Anteriorly, the muscle inserts as one bundle on the medial epiphysis of the basal tubera with a lateral tendon that starts at C4.

b) Longus cervicus (medialis + lateralis)

Originates posteriorly from the 13th flat intercentrum between D4 - D5, and inserts on the second intercentrum (lateral projection) (plate 3.5d). The muscle is divided into two sections (plate 3.5b): the medialis section originates from the 6th intercentrum (= 4th keeled intercentrum) between C5-C6 and on the rib ligament of C6, and runs anteriorly with slips from the keeled intercentra of C3-5. It ends on the central ridge of the second intercentrum (C2). The lateralis section originates from the 13th flat intercentrum between D4 -D5, and runs anteriorly with slips from the intercentra and rib ligaments of D5-C6. The muscle also originates from the first, second and third cervical ribs by a tendinous sheet with a final insertion on the axis transverse process and the lateral projection of the second intercentrum.

8- First flat intercentral muscle slip to basioccipital

Ventrally, the muscle originates from the flat first intercentrum (shallow groove), and inserts on the basal tubera deep to the longus colli.

9- Third intercentral muscle slip to basioccipital

Ventrally, the muscle originates from the anterior edge of the third intercentrum (= first keeled intercentrum), and inserts on the basal tubera between the first intercentrum muscle and the longus colli (deep to longus colli) (Fig. 3.3).

Very deep muscles

1- Axis to atlas neural arch muscle

See chapter 1.

2- Interspinalis, interneural arch and interzygapophyses

See chapter 1.

3- Cervical and trunk central tendon

A tendon that extends posteriorly along the flat intercentra and centra of the last cervical and dorsal vertebrae. The tendon attaches to the last keeled intercentrum.

Special anatomical features in *Sphenodon punctatus*

The following characters were observed uniquely in *Sphenodon punctatus*, or are found randomly in other groups.

Osteology

Skull

1- The parietal lateral processes are short relative to the elongated dorsal process of the squamosal.

2- The squamosal is a large quadriradiate bone.

3- The supraoccipital bears a posteromedian bony process (for axis muscle attachment).

4- The exoccipital is not fused to the opisthotic.

Presacral vertebrae

1- A proatlas is present.

2- The atlantal arch possesses anterior and posterior projections.

3- The axis centrum has a bony crest above the transverse process (where longissimus capitis 3 originates).

4- The posterior neural spines of the cervical vertebrae are wavy with ridges (where splenius capitis and spinalis/semispinalis cervicus muscle slips attach).

5- The first and second intercentra are flat.

6- The first and second flat intercentra are followed by seven keeled intercentra, then simple flat intercentra (crescent-shaped) run through to the caudal region.

7- The ribs possess uncinate processes.

8- Rib ratio = 2 + 1 + 4 +1 (ribless, short, medium, long). The first cervical rib is bicipital.

Myology

Superficial muscles

1- Trapezius inserts on the clavicle.

2- Sub-iliocostalis rib muscles connect the uncinate processes to the gastralia.

Intermediate muscles

1- The episternocleidomastoid branches anteriorly to insert in three areas on the skull; the paroccipital process, squamosal, and squamosal/parietal.

Deep muscles

1- An axis to supraoccipital muscle is present.

2- Splenius capitis has superficial tendon slips that originate from the dorsal and cervical neural spine tips, and deep muscle slips from the cervical spines.

3- Longissimus cervicus is divided into anterior (proatlas) + posterior (atlas) bundles.

4- Ventrally, the third intercentral muscle to basioccipital (= first keeled intercentrum) muscle inserts superficial to the first intercentral to basioccipital muscle, and deep to the longus colli.

5- Longus cervicus (originating from the D4-D5 intercentrum) is longer than longus colli (originates from the 11th intercentrum between D2-D3).

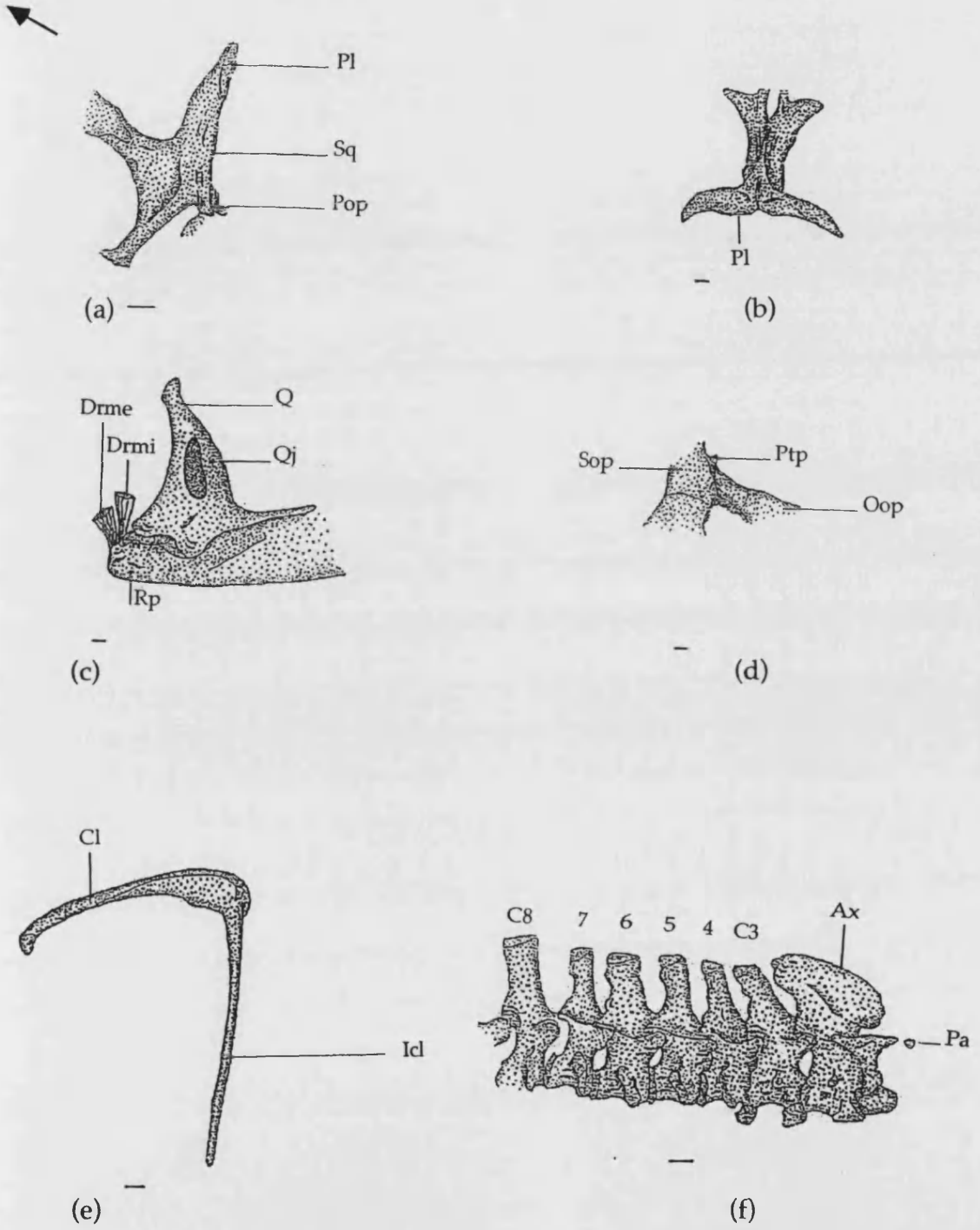


Plate (3.1) *Sphenodon punctatus*, a) left posterolateral view of the squamosal (Sq); b) dorsal view of the parietal (Pl); c) right lateral view of the quadrate (Q) and quadratojugal (Qj). d) left posterolateral view of dorsal braincase showing the posterior process (Ptp) on the supraoccipital (Sop); e) lateral view of the clavicle (Cl) and T-shaped interclavicle (Icl); f) right lateral view of cervical vertebrae (C1-8) and proatlas (Pa). Scale bar = 1 mm.

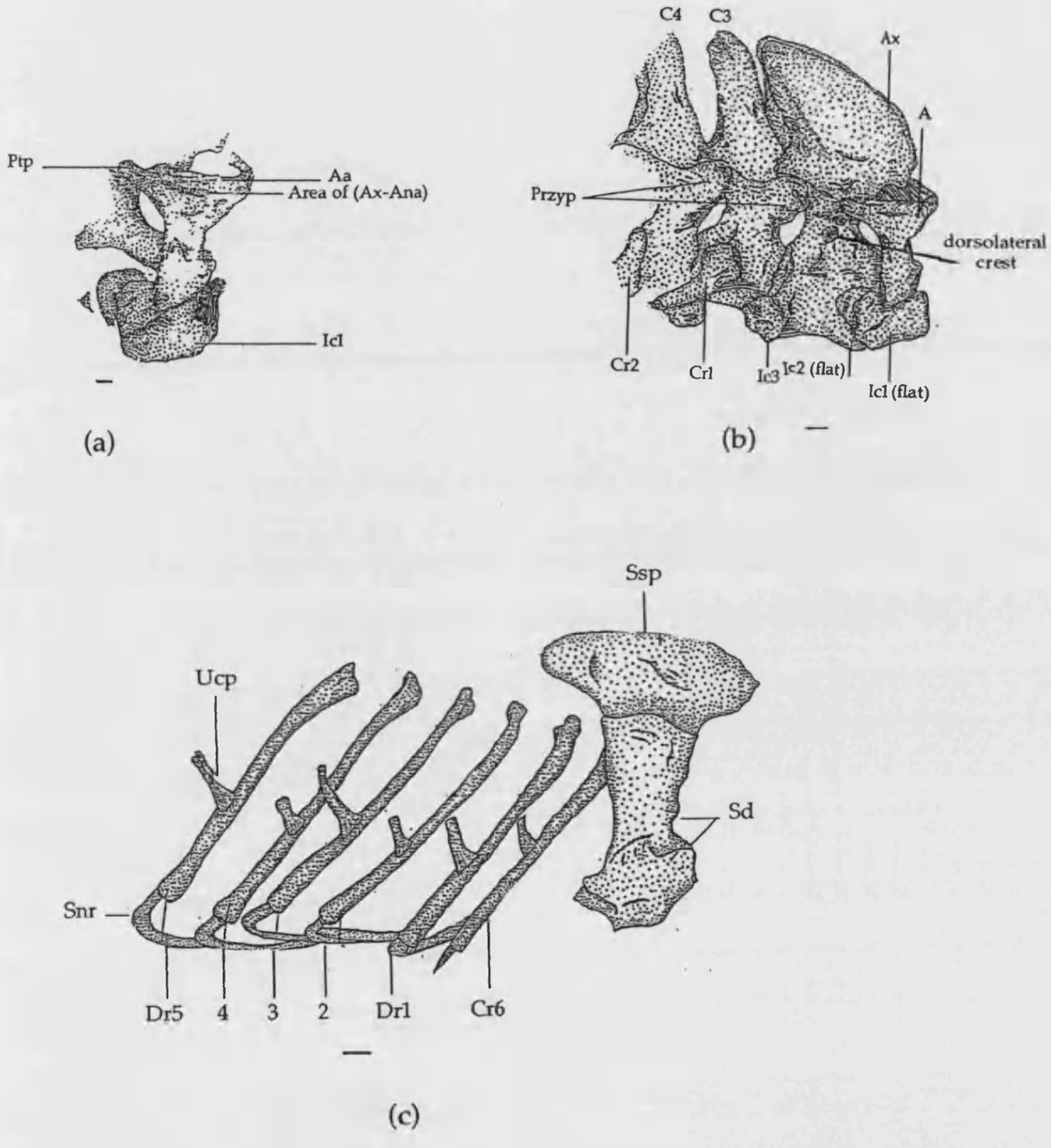


Plate (3.2) *Sphenodon punctatus,* a) right lateral view of the atlas with elongated posterior processes (Ptp) and flat intercentrum (Ic1); b) right lateral view of the anterior cervical vertebrae showing the prezygapophyses processes (Przyp) and first & second flat intercentra (Ic1-2) ; c) right lateral view of the pectoral girdle, sternal ribs (Snr) with uncinate process (Ucp). Atla = A; Axis = Ax. Scale bar = 1 mm.

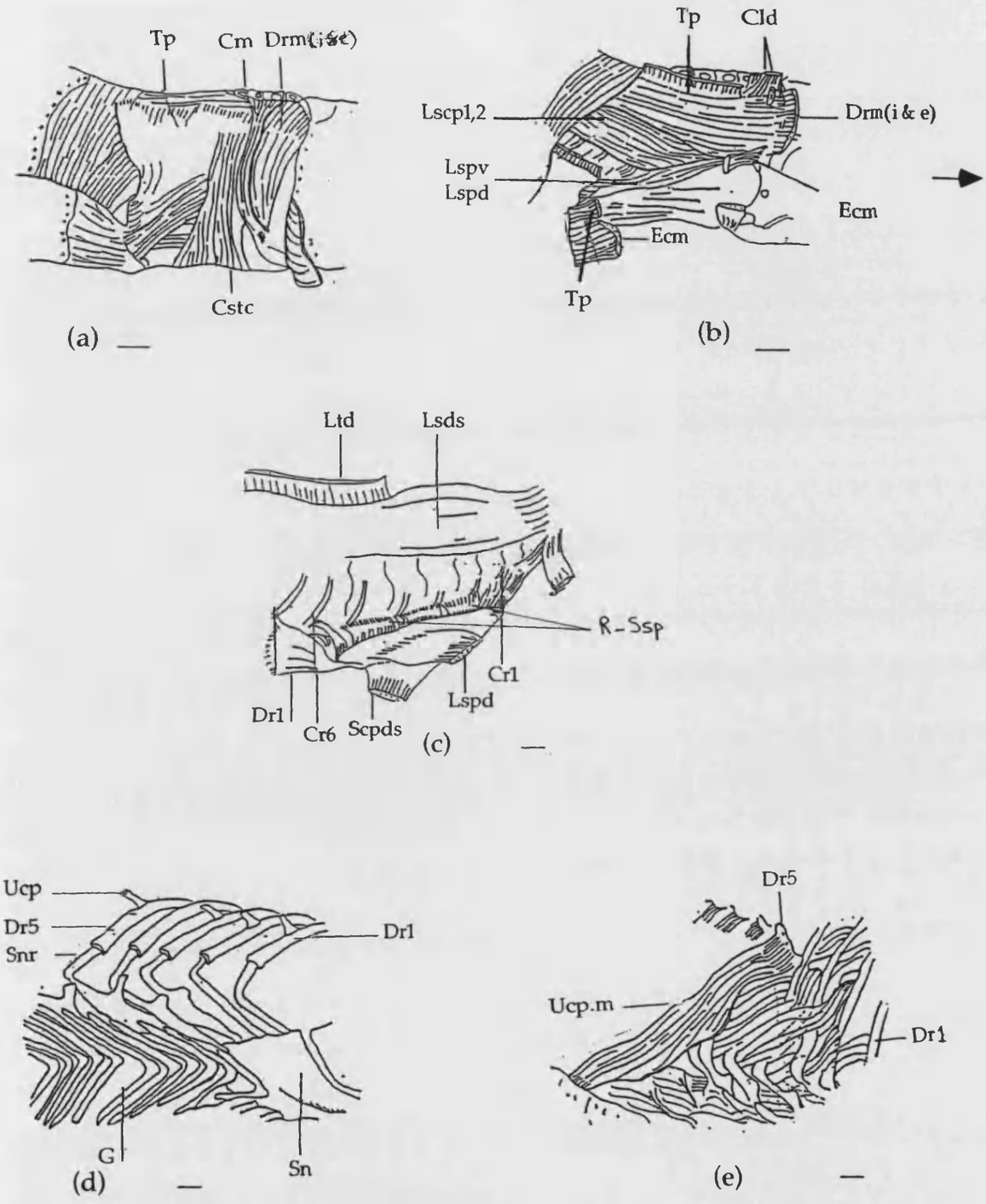
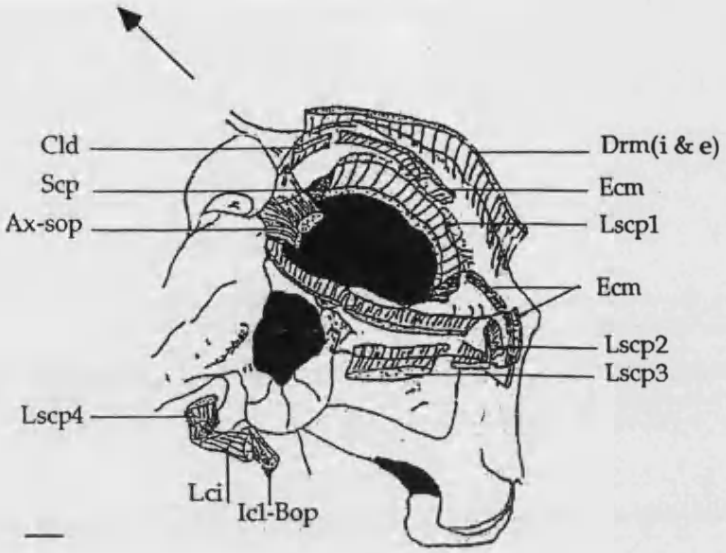


Plate (3.3) *Sphenodon punctatus*, a) right lateral view of the craniocervical region with most superficial muscles like depressor mandibular externus and internus (Drme & Drmi) and trapezius (Tp); b) right dorsal view of craniocervical region showing the trapezius, clavicle dorsalis (Cld) and deep muscles like longissimus capitis 1 and 2 (Lscp1 & Lscp2); c) right dorsal view of the neck region showing ribs to suprascapula muscle slips (R-Ssp); d) right ventral view of the sternum (Sn) and sternal ribs (Snr) with uncinate processes (Ucp), gastralia (G); e) right ventral view of the trunk showing extension of the uncinate process muscle slips (Ucpm) along gastralia and sternal ribs. Scale bar = 1 mm.



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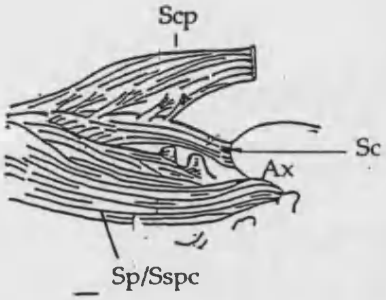

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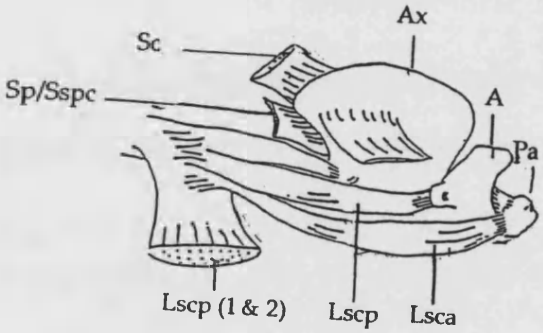

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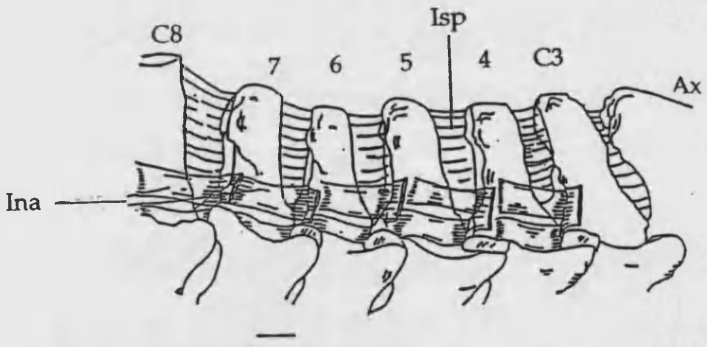
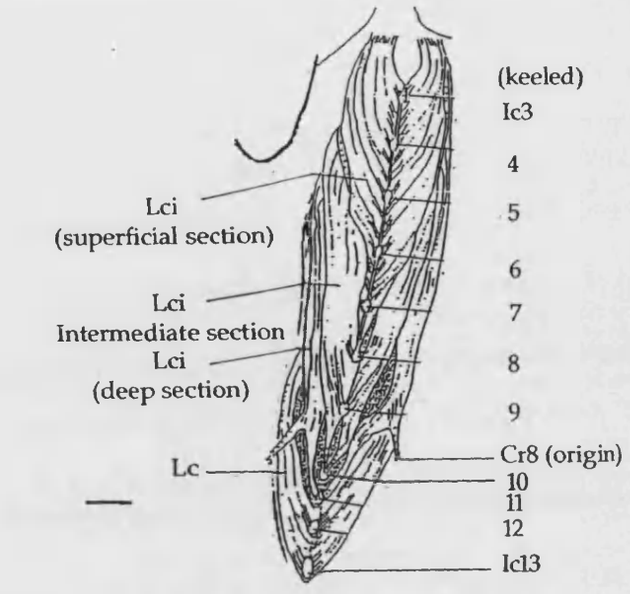


(d)

Plate (3.4) *Sphenodon punctatus*, a) left posterolateral view of the skull showing most deep muscles inserting on the occipital surface of the skull; b) right lateral view of the anterior cervical vertebrae showing the mode of origin of splenius cervicus (Sc) and capitis; c) right lateral view of anterior cervical vertebrae showing the insertion of the longissimus cervicus anterior (Lsca) (on proatlas = Pa) and posterior (Lscp) (on atlas = A). d) right lateral view of the cervical vertebrae showing the inter-neural arch, inter-spinalis muscle slips (Ina & Isp). Scale bar = 1 mm.



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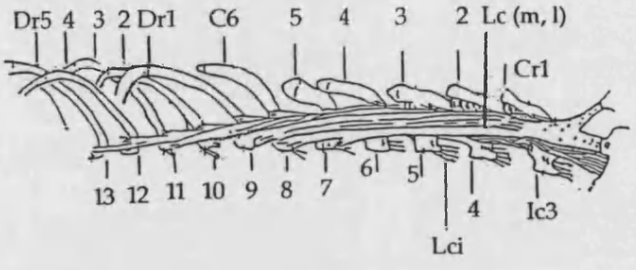

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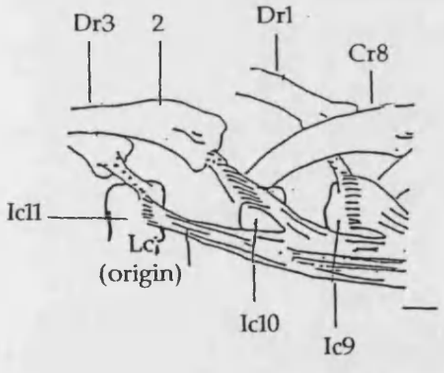
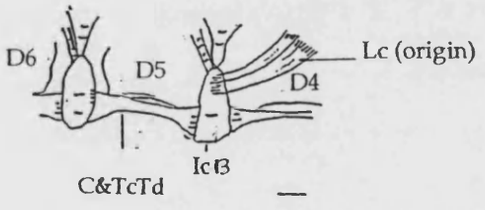




(c) (d)

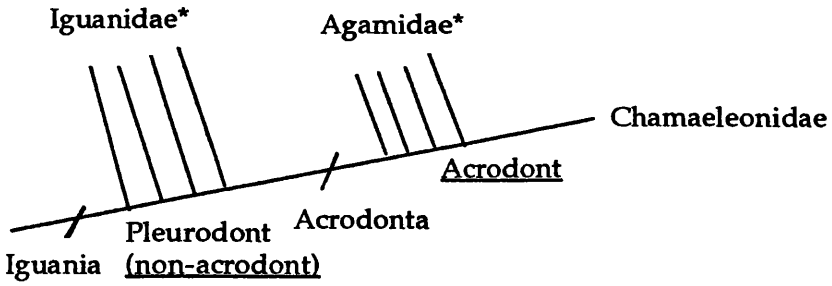
Plate (3.5) *Sphenodon punctatus*, a) ventral view of longus colli (Lci) origin, extension in division and insertion; b) right ventrolateral view of the cervical and dorsal vertebrae showing the origin, extension and insertion of longus cervicus (Lc) and the mode of attachment of longus cervicus on the anterior cervical ribs and intercentra; c) right ventrolateral view of dorsal vertebrae showing start of longus colli (Lci) from intercentrum 11; d) the tendon along the cervical and trunk centra (C&TcTd), also the start of longus cervicus from Ic13. Scale bar 1 mm. Scale bar = 1 mm.

CHAPTER (4)

IGUANIA

Iguania is the sister group of all other squamates (Scleroglossa), and represents one of the phylogenetic lineages that radiated during the Jurassic (Estes, 1983; Zug, 1993).

Within the Iguania, the Chamaeleonidae (Rhiptoglossa - Camp, 1923) are more closely related to Agamidae* than to Iguanidae* (Camp, 1923; Moody, 1980; Rieppel, 1981) on the basis of the acrodont dentition and many other features (Moody, 1980). The iguanids are probably not a monophyletic group but rather are a mixed set of pleurodont lineages lacking the derived characters of agamids + chamaeleons. Similarly, agamids do not form a monophyletic family, but are a set of acrodont lineages which lack the derived characters of chamaeleons. This is shown diagrammatically below and denoted by placing an asterisk after Iguanidae* and Agamidae* in the text. Most iguanians have stout bodies with long tails and long legs, and a rough body surface with overlapping scales (Zug, 1993).



The paraphyletic status of Iguanidae* and Agamidae*

Family: Iguanidae*

Iguanids are primarily a New World group, but one genus occurs in Fiji and the Tonga Islands, and two genera are found on Madagascar (Webb et al., 1978; Young, 1981; Zug, 1993). The iguanids are a highly diverse group of

about 50 genera and more than 700 species, subdivided into a number of distinct lineages (Zug, 1993). A few iguanids are herbivores, one is marine, but most are insectivores and occupy terrestrial (forest and desert environments) and arboreal niches. Their size ranges from small (9~ 100mm) to very large (1.2 ~ 1.5m), and all have a long tail and well-developed limbs. The teeth are attached to the lingual side of the jaws (pleurodont) (Webb et al., 1978; Zug, 1993).

Examples include: *Anolis,* a common North, Central and South American lizard, *Iguana* of South and Central America; the marine iguana *Amblyrhynchus;* the Horned lizard *Phrynosoma;* and the Malagasy iguanids - *Chalarodon* and *Oplurus* (Young, 1981; Zug, 1993).

Family: Agamidae*

Agamids are found in the warmer parts of the Old World such as South East Europe, Asia, Australia and Africa (excluding Madagascar). There are about 40 genera and 320 species, which vary in both shape and size. Agamids are mainly insectivorous, and are terrestrial to arboreal lizards with well-developed legs and long tails (Webb et al., 1978). In agamids most of the teeth are fused to the crest of the jaws (= acrodont) (Young 1981; Zug, 1993).

Examples include: *Pseudocalotes dringi*, from the mountain forest of western Malaysia (Hallermann and Bohme, 2000); the spiny lizards of North Africa and Indian deserts, *Uromastyx;* the gliding Indo-Malayan genus *Draco,* the Australian frilled *Chlamydosaurus* and *Amphibolorus;* the Toad-headed *Phrynocephalus;* the slender-bodied *Agama,* and the spiny, desert-living, short-limbed Australian *Moloch* (Webb et al., 1978; Young, 1981; Zug, 1993).

Family: Chamaeleonidae

Chameleons are most diverse in Africa and Madagascar, although they are also found in southern India, Arabia and southern Spain (Webb et al., 1978).

These are highly modified arboreal lizards, with 6 genera and about 88 species. They feed mainly on insects, particularly flies, by means of a very long adhesive club-tipped tongue (Young, 1981; Zug, 1993). These peculiar lizards have laterally compressed bodies, cranial casques or one or more horns on the snout, prehensile tails, opposable digits for grasping branches, large independently movable eyes, no tympanic cavity, and granular skin capable of changing colour as a result of temperature and other environmental or mood changes, e.g. catching a fly. In chameleons the teeth are acrodont, as in Agamidae* (Webb et al., 1978; Young, 1981; Zug, 1993). Chamaeleonidae includes the widespread *Chamaeleo* (e.g. the three horned *Chamaeleo jacksonii* and the flap necked *Chamaeleo dilepis);* the South African ovoviviparous *Bradypodion;* the small oviparous rain forest chameleons *Brookesia,* of Madagascar; and *Rhampholeon* of Africa (Zug, 1993; Rieppel and Crumly, 1997).

Anatomy of the neck region in Iguanidae*

I dissected *Oplurus cyclurus, Iguana iguana, Crotaphytus collaris, Phrynosoma platyrhinos* and *Anolis richardii. Anolis* was examined in the greatest detail.

Anolis richardii = (male).

A. edwardsii = (skeleton).

A. biporcatus = (female skeleton).

Previous works:

Nopcsa, 1928; Oelrich, 1956; Etheridge, 1964; Blanc, 1965; Hoffstetter and Gasc, 1969; De Queiroz, 1987; Etheridge and De Queiroz, 1988; Frost and Etheridge, 1989.

Osteology of *Anolis richardii*

(Plate 4.1.1)

Skull

1- Parietal

The bone possesses long wide posterior processes (where depressor mandibulae internus, clavicle dorsalis and longissimus capitis 1 attach) that extend laterally towards the temporal arch units. The mid-posterodorsal margin possesses a short median process flanked by shallow concavities (where splenius capitis inserts).

2- Squamosal

This is a long slightly curved narrow bone that retains a dorsal process (for depressor mandibulae internus origin). (Nopcsa, 1928; Oelrich, 1956 – *Ctenosaura pectinata;* Blanc, 1965 – *Chalarodon madagascariensis*).

3- Supratemporal

This elongated flat bone extends along the antero and posteroventral sides of the parietal posterior processes (where depressor mandibulae internus originates) (De Queiroz, 1987; Etheridge and De Queiroz, 1988).

4- Quadrate

A thick elongated bone with dorsal condyles.

5- Retroarticular process

This is well-developed with a wide posterior end. It possesses a dorsal concavity (where depressor mandibulae inserts).

6- Supraoccipital

This flat bone has a long, shallow midline ridge (where splenius capitis muscle inserts), that reaches the processus ascendens dorsally, and the foramen magnum ventrally (Fig., 4.1.1 b). The lateral margin has a shallow dorsal ridge (where rectus capitis inserts).

7- Oto-occipital

The paroccipital process is narrow with a ventrolateral extension (episternocleidomastoid insertion). Posteriorly, the arms have a deep concave surface (where longissimus capitis 2 and episternocleidomastoid insert). The ventrolateral margin of the oto-occipital is convex (where intercentral muscle slips extend toward the long crista tuberalis).

8- Paroccipital epiphyses

Absent.

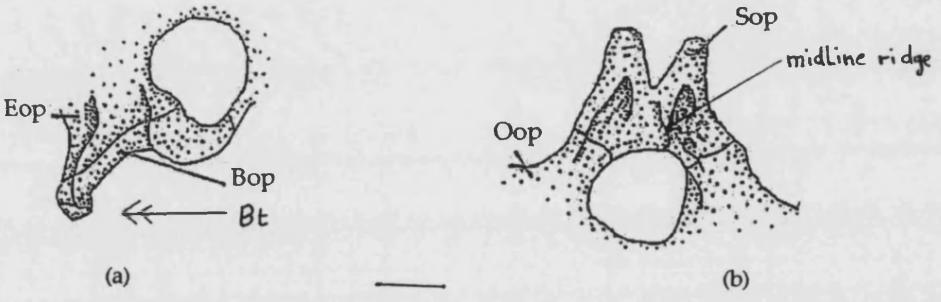


Fig. (4.1.1) *Anolis edwardsii*, occipital view of the skull showing; a) The basioccipital (Bop) with triangular basal tubera (Bt), b) The supraoccipital (Sop) with a midline ridge. Oto-occipital = Oop. Scale bar = 1 mm.

9- Basioccipital

The basal tubera are triangular (where longus colli and longissimus capitis 4 insert) (Fig., 4.1.1 a). The surface between the basal tubera retains a linear ridge (where the first superficial intercentrum to basioccipital muscle inserts).

Presacral vertebral column

1- Atlas

The posterior process is long (longissimus cervicus insertion) whereas the centrum possesses a wide transverse process (where levator scapula dorsalis and ventralis originate) and a keeled intercentrum (where the first intercentrum to basioccipital/oto-occipital muscle originates) (plate 4.1.1a).

2- Axis

The neural spine has a triangular posterodorsal process (where spinalis cervicus inserts). The postzygapophysis is horizontal with a tubercle (where spinalis cervicus attaches) (plate 4.1.1a). The transverse process projects strongly (iliocostalis major). Ventrally, the centrum has two keeled intercentra. The second intercentrum is smooth, and the third intercentrum is fused to the centrum in front (C2) (plate 4.1.1a).

3- C3-C8

There are 8 cervical vertebrae (Hoffstetter and Gasc, 1969) and about 5 keeled intercentra (plate 4.1.1b). However, Blanc (1965) described only 4 intercentra sutured between centra in *Chalarodon madagascariensis*. The neural spines are wide and short with a pointed dorsal edge and triangular tips which are concave posteriorly (where spinalis/semispinalis muscles attach). The anterior and posterior margins of the spines are smooth, and they are inclined relative to the long axis of the centrum. The height of the spines increases posteriorly towards the anterior dorsal spines (where the splenius capitis originates). The centra are long (C3-5), then become shorter (C6-8), and finally become long again along the trunk region. Ventrally, the centra are keeled between the smooth shallow intercentra (where longus colli and cervicus run). The intercentra are fused to the centrum in front (Hoffstetter and Gasc, 1969).

4- The anterior dorsal vertebrae

The neural spines are wide and have a compressed tip (where spinalis semispinalis muscle complex attaches) with smooth, curved anterior and posterior margins.

5- Ribs

The first rib starts on C5 (cervical rib ratio of 4 + 2 +2) (Frost and Etheridge, 1989) (plate 4.1.1b). The distal end of the first cervical rib is pointed with a

cartilaginous end, while that of the second rib is wide. The posterior cervical ribs are long and again pointed, with cartilaginous ends (Etheridge, 1964 – *Sceloporus;* Camp, 1923). The rib ligaments connect the ribs to the centra (not to the intercentra).

Pectoral girdle

1- Sternum

Well - developed.

2- Clavicle

This elongated curved bone articulates with the suprascapula/scapula (where trapezius inserts). It meets the interclavicle ventrally, and has a narrow non-perforated medial end (Etheridge and De Queiroz, 1988).

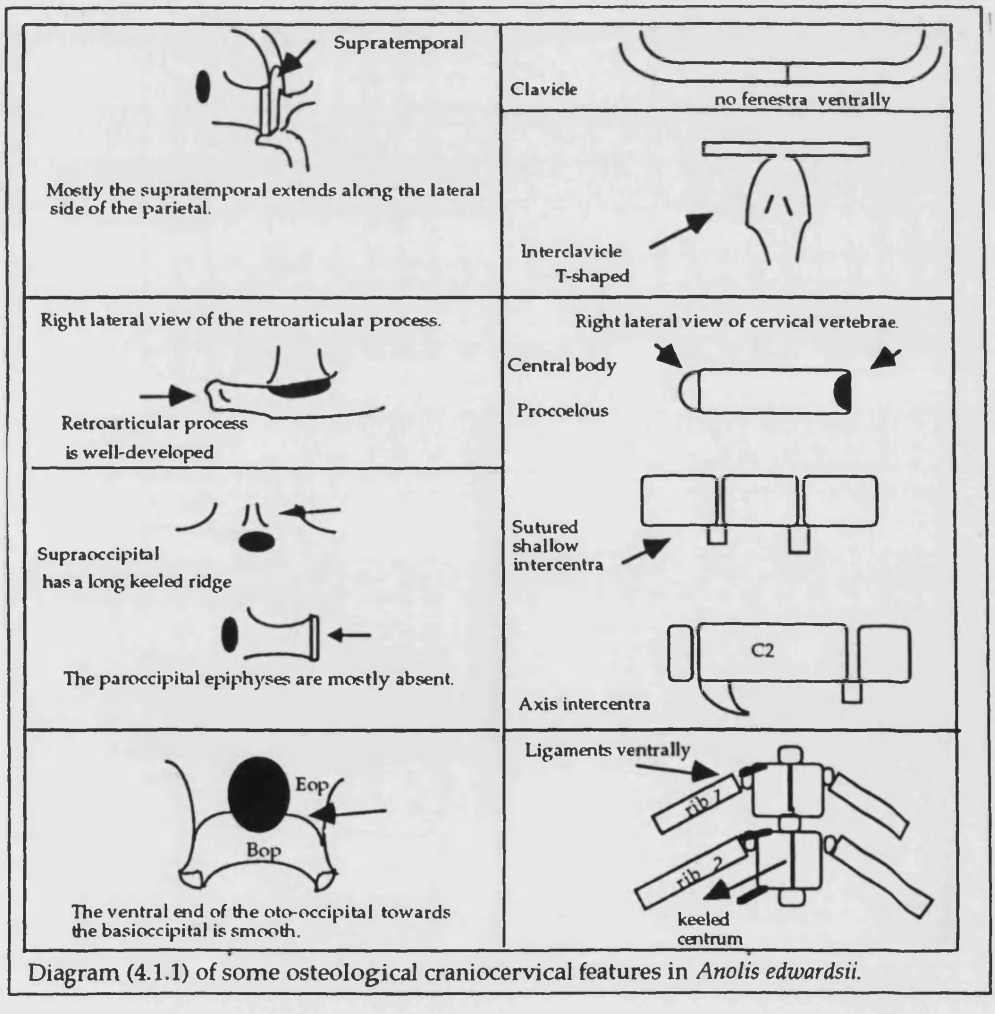


Diagram (4.1.1) of some osteological craniocervical features in *Anolis edwardsii.*

3- Interclavicle

This is a flat T-shaped bone with a reduced anterior process (plate 4.1.1c) (Etheridge and De Queiroz, 1988; Frost and Etheridge, 1989), long lateral pointed arms (where episternocleidomastoid originates) and a long wide posterior process (Etheridge, 1964 – *Sceloporus*).

3- Scapulacoracoid and suprascapula

The coracoid is well developed with fenestrae ventrally. The scapula is wide with a wide dorsal cartilaginous suprascapula (plate 4.1.1d)(where ribs to suprascapula muscle slips insert).

Muscles of *Anolis richardii*

(Plate 4.1.2 - 4.1.3 – 4.1.4)

Superficial muscles

1- Depressor mandibulae internus and externus

The internus branch originates broadly from the skull roof (parietal + supratemporal), while the externus branch originates from the parietal and adjacent muscle fascia. Both muscles insert on the well-developed retroarticular process (overlapping each other) (Oelrich, 1956 – *Ctenosaura pectinata*).

2- Cervicomandibularis

Originates from muscle fascia dorsally, and inserts on the mandible under the retroarticular process of the articular (plate 4.1.2a).

3, 4- Constrictor colli and latissimus dorsi

See chapter 1.

5- Trapezius

Originates from muscle fascia dorsally and tapers to insert at the anterior junction of the scapula and clavicle (plate 4.1.2e).

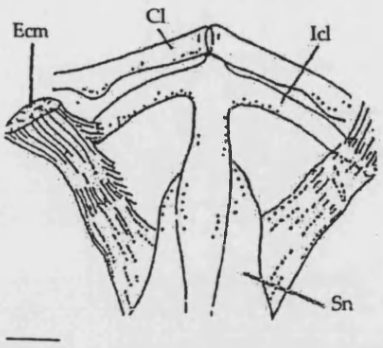


Fig. (4.1.2) *A. richardii*, ventral view of the pectoral girdle shows the origin of episternocleidomastoid (Ecm) from interclavicle (Icl) & sternum (Sn). Scale bar = 1 mm.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arm of the interclavicle (muscle fibres) and the sternum (tendon) (Fig., 4.1.2), and inserts on the lateral margin of the paroccipital process.

2- Clavicle dorsalis

Originates from the posterolateral edge of the parietal and dorsal muscle fascia (plate 4.1.2d), and inserts on the anterior surface of the clavicle.

3- Levator scapula dorsalis and ventralis

Both muscles originate from the atlas transverse process, and insert on the suprascapula (plate 4.1.2e) such that: the dorsalis branch inserts on the anterior side of the suprascapula, and the ventralis branch inserts below the dorsalis on the anteroventral edge of the suprascapula.

4- Ribs to suprascapula muscles

The muscle slips originate from the distal end of the first, second and third cervical ribs, and insert on the anterior and dorsal edges of the suprascapula (plate 4.1.3a-c). The third and fourth cervical rib muscle slips insert on the posterior edge of the suprascapula. The deep second cervical rib muscle inserts on the anteromedial surface of the suprascapula (Fig., 4.1.3).

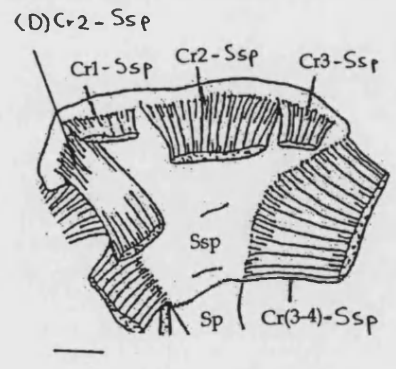


Fig. (4.1.3) *A. richardii*, left lateral view of the pectoral girdle showing superficial and deep rib to suprascapula muscle slips; Cr(1-4)-Ssp &(D)Cr2-Ssp. Scale bar = 1 mm.

Deep muscles

1,2 - Obliquus and rectus capitis

The obliquus capitis originates from the axis neural spine, and extends anteriorly as one thick layer to insert on the superior side of the paroccipital process. The rectus capitis originates from the atlantal arch and the dorsal side of the axis neural spine, and inserts on the ventrolateral margin of the supraoccipital (shallow ridge) (Oelrich, 1956).

3- Splenius capitis

Originates from the neural spines of D1-D3, and the muscle fascia of longissimus dorsi (plate 4.1.3d). It extends as one single trunk to insert on the posterodorsal side of the parietal and supraoccipital, under the insertion of episternocleidomastoid and constrictor colli (Oelrich, 1956). The muscle branches anteriorly along C3 - C4 to attach to longissimus capitis 1.

4- Spinalis/semispinalis muscles

B,c,d) Spinalis cervicus, Spinalis/semispinalis cervicus, Spinalis/ semispinalis complex

See chapter 1.

5- Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus cervicus

Branches from longissimus dorsi along C4, and inserts on the atlas posterior process (See chapter 1).

c) Longissimus capitis 1

Branches anteriorly from longissimus dorsi along C4, and inserts on the dorsolateral side of the parietal.

d) Longissimus capitis 2

Branches from longissimus dorsi along C3, and inserts on the lateral side of the paroccipital process, internal to the episternocleidomastoid origin.

e) Longissimus capitis 3

Absent.

f) Longissimus capitis 4

Branches laterally from longissimus dorsi along C5, and inserts on the external side of the basal tubera, lateral to the longus colli insertion.

g) Longissimus capitis minor

Originates from the atlas posterior process, and runs parallel with longissimus capitis 4 to insert on the ventrolateral tip of the oto-occipital (straight) close to the basal tubera (Fig., 4.1.4).

6) Iliocostalis muscles

a, b) Iliocostalis major and Iliocostalis cervicus

See chapter 1.

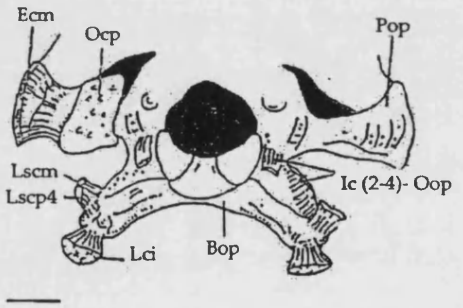


Fig. (4.1.4) *A. richardii,* occipital view of the skull showing deep muscles such as obliquus capitis (Ocp), longissimus capitis 4 & minor (Lscp4 & Lscpm), intercentral muscle to oto-occipital muscle slips (Ic[2-4]-Oop) & longus colli (Lci). Scale bar = 1 mm.

7- Longus muscles

a) Longus colli

Originates laterally from the D1 rib ligament (tendinous bundle), and runs anteriorly and laterally along C6-8. The muscle then originates from the mid-intercentral apices of C2-5. The two parts run toward the skull where they finally insert on the basal tubera (tendinous insertion) (plate 4.1.4b).

b) Longus cervicus

Originates from C7 centrum and the C8 rib ligament and runs anteriorly taking slips from C4-7 rib ligaments to insert on the posterior surface of the second and third intercentra (plate 4.1.4c, d).

8- First intercentral muscle slip to basioccipital and oto-occipital

Originates from the first keeled intercentrum, and inserts on the central area of the basioccipital (superficial) and towards the crista tuberalis of the oto-occipital (deep).

9- Posterior (2-4) intercentral muscle slips to oto-occipital

The intercentral muscles originate from the 2-4 intercentra, and diverge wide anteriorly along the convex ventrolateral margin of the oto-occipital, towards the cristae tuberalis laterally and the paroccipital process dorsally. Ventrally, the muscle slips insert superficial and lateral to the deep first intercentrum Fig. (4.1.4).

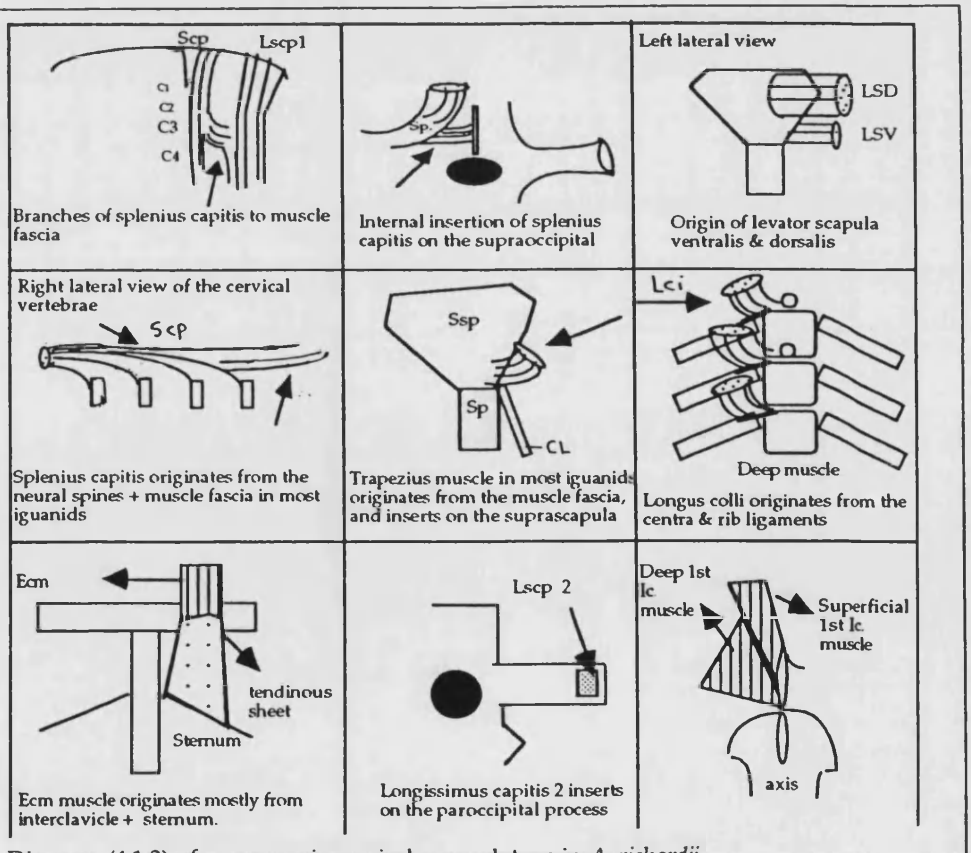


Diagram (4.1.2) of some craniocervical musculature in *A. richardii*.

- Ventrally, the posterior intercentral muscle slips insert wide on the ventrolateral side of the oto-occipital close to the cristae tuberalis of the oto-occipital, and sometimes towards the basioccipital.

2) Variation between iguanids examined:

(Plate 4.1.5 – 4.1.6 – 4.1.7)

- In *Phrynosoma*, the squamosal is wide, while in all iguanids examined the squamosal is narrow with posterior dorsal and ventral processes.
- In *Phrynosoma*, the supratemporal extends below the parietal posterolateral processes (Frost and Etheridge, 1989), while in all examined iguanids it extends along the lateral side of the parietal posterolateral processes.
- Zygosphenes and zygantra are absent in most examined iguanids except *I. iguana.*
- There are 5 keeled intercentra in *I. iguana, P. platyrhinos* and *A. richardii,* and are 6 in *O. cyclurus* and *C. collaris.* The intercentra are sutured between the central bodies, except in *A. richardii* where they are fused to the centrum in front (Hoffstetter and Gasc, 1969).
- In *O. cyclurus, A. richardii, A. edwardsii, A. biporcatus* and *I. iguana,* the first cervical rib starts on C5 (rib ratio = 4+2+2) (Frost and Etheridge, 1989) , while in *C. collaris* and *P. platyrhinos,* the cervical rib begins on C4 (rib ratio = 3+3+2).
- In *I. iguana, O. cyclurus* and *C. collaris,* the depressor mandibulae externus originates from the parietal, while in *A. richardii* it arises from parietal + muscle fascia and in *P. platyrhinos* it originates from the squamosal.
- In most iguanids examined the trapezius originates from the muscle fascia of splenius capitis, except in *O. cyclurus,* where it originates from

the spine tips in the mid-dorsal line (plate 4.1.5b). The muscle usually inserts on the suprascapula, except in *A. richardii* where it inserts on the clavicle + scapula.

- In *A. richardii*, *C. collaris* and *P. platyrhinos*, the episternocleidomastoid originates from the interclavicle and sternum (plate 4.1.6c), or from the interclavicle only as in *O. cyclurus* and *I. iguana*. The muscle usually inserts on the paroccipital process and skull roof, except in *A. richardii* where it inserts on the paroccipital process.
- In *A. richardii* and *I. iguana*, the clavicle dorsalis originates from the muscle fascia and parietal, but from muscle fascia only in *O. cyclurus* (plate 4.1.5c). In *P. platyrhinos*, the muscle originates from the squamosal and inserts on the interclavicle (plate 4.1.6b).
- Ribs to suprascapula muscle slips usually originate from cervical vertebrae, except in *O. cyclurus*, where they arise from cervical and dorsal ribs.
- The atlas to cervical rib muscle is present only in *I. iguana*. It originates from the anterior edge of the third cervical rib (=C7 rib), and inserts on the atlas transverse process (plate 4.1.5d).
- Obliquus capitis usually inserts as one layer on the paroccipital process, except in *P. platyrhinos* where it inserts as two layers (externus dorsal layer + internus ventrolateral layer) (L-shaped insertion) (plate 4.1.7b).
- Splenius capitis usually originates from the neural spines and muscle fascia and runs anteriorly as a single bundle. It is divided anteriorly to insert on the muscle fascia of longissimus capitis 1 before inserting on the parietal and supraoccipital (midline ridge) (plate 4.1.7d). While in *P. platyrhinos* the muscle originates from the neural spines only and runs anteriorly to join a deep bundle from the spinalis cervicus along C2. It is

non-branched anteriorly, and inserts (superficial + deep) on the parietal and dorsal edge of the supraoccipital (plate 4.1.7a, c).

- Longissimus capitis 1 usually inserts on the parietal, except in *P. platyrhinos* where it inserts on the parietal and paroccipital process (plate 4.1.7b, c).
- Longissimus capitis 2 is present, except in *P. platyrhinos*.
- Longissimus capitis 3 is absent, except in *I. iguana*.
- Ilicostalis cervicus usually runs anteriorly to insert on the atlas transverse process as a single tendinous bundle, except in *P. platyrhinos* where it inserts as 2 bundles = dorsalis + ventralis.

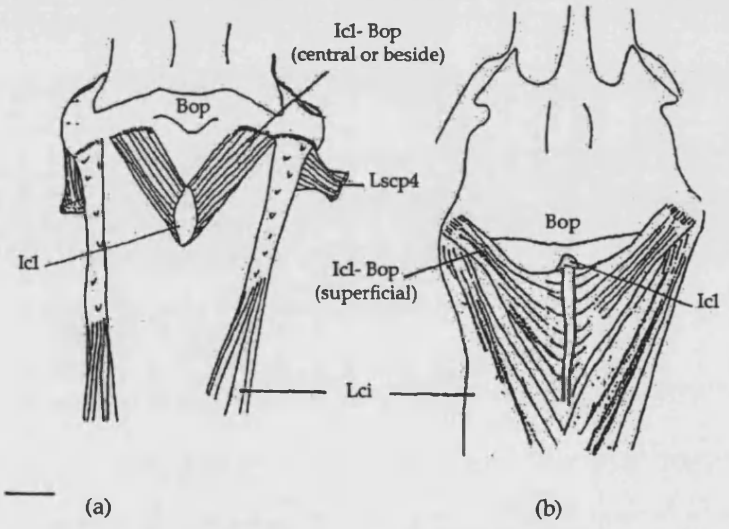


Fig. (4.1.5) Ventral view of the craniocervical region in; a) *P. platyrhinos*, showing the central insertion of the 1st intercentral muscle to basioccipital (Ic1-Bop); b) *I. iguana*, where 1st intercentral muscle slip (Ic1-Bop) inserts partially superficial to longus colli (Lci). Scale bar = 1 mm.

- In *A. richardii*, *I. iguana* and *O. cyclurus*, the longus cervicus originates from the cervical vertebrae, while in *C. collaris* and *P. platyrhinos* it arises from the dorsal vertebrae. The longus cervicus starts from centra and rib ligaments in *O. cyclurus*, *A. richardii* and *P. platyrhinos*, but in *I. iguana* and *C. collaris* it starts from rib ligament only. The muscle is shorter than the longus colli, except in *I. iguana* where they are equal in length .

- The superficial branch of the first intercentrum to basioccipital/oto-occipital muscle inserts on the central area of the basioccipital beside longus colli, except in *I. iguana* where the muscle inserts laterally and is partially superficial to the longus colli.
- In *A. richardii, O. cyclurus* and *C. collaris,* the posterior intercentra muscle slips insert on the oto-occipital only, while in *I. iguana* and *P. platyrhinos* they insert on the basioccipital and oto-occipital. The number of intercentral muscle slips to the skull is usually 4, except *A. richardii* where it is 3.
- The cervical and trunk central tendon was present in all taxa examined except *P. platyrhinos* and *C. collaris.*

ANATOMY OF THE NECK REGION IN AGAMIDAE*

The species dissected were *Agama agama, Calotes versicolor, Ceratophora stoddarti, Draco fimbriatus, Moloch horridus, Phrynocephalus maculatus, Pogona sp.,* and *Uromastyx aegyptia microlepis,* only *Uromastyx* (juvenile and adult) was examined in detail.

U. aegyptia microlepis (juvenile, adult and adult skeleton)

Previous works:

Beddard, 1905; Broom, 1925; El-Toubi, 1945, 1947; Islam, 1956; Tilak, 1964; Hoffstetter and Gasc, 1969; Kalil et al., 1977; Moody, 1980; Wahba et al., 1992a.

Osteology of *Uromastyx aegyptia microlepis* (Juvenile)

(Plate 4.2.1)

Skull

1- Parietal

The posterodorsal margin is straight with long posterolateral processes (where depressor mandibulae externus originates and longissimus capitis 1 insert).

2- Squamosal

This long curved bone bears a strong dorsal process (plate 4.2.1b) (Islam, 1956; Tilak, 1964) (where depressor mandibulae externus originates). The bone meets the parietal, supratemporal and quadrate, but not the paroccipital process (Broom, 1925).

3- Supratemporal

This small bone appears posteriorly between the parietal dorsally; quadrate ventrally; paroccipital process internally and squamosal externally. It is located below the posterior parietal process (where depressor mandibulae originates). Beddard (1905) did not identify the bone in the skull of *Uromastyx*.

4- Quadrate

The wide body possesses a slightly exposed posterodorsal process (where depressor mandibulae internus originates).

5- Retroarticular process

The retroarticular process is well-developed with a wide posterior end (where depressor mandibulae branches insert).

6- Supraoccipital

This has a smooth posterior surface (where rectus capitis inserts).

7- Oto-occipital

The paroccipital process is narrow (where episternocleidomastoid inserts laterally) and has a slightly concave superior surface (where longissimus capitis 2 inserts). Laterally, the process articulates with the quadrate, squamosal, supratemporal and parietal (Tilak, 1964). The ventrolateral

margin of the oto-occipital possesses a long narrow crista tuberalis (plate 4.2.1a) (where intercentral muscle slips insert widely).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera have triangular epiphyses (where both longus colli and longissimus capitis 4 insert).

Presacral vertebral column

1- Atlas

Laterally, the posterior processes are short (where longissimus cervicus inserts) and the transverse processes are wide (levator scapula dorsalis and ventralis originate). The intercentrum is keeled (superficial and deep intercentral muscles to basioccipital/oto-occipital originate) (plate 4.2.1c).

2- Axis

The posterodorsal edge of the neural spine is triangular (where spinalis muscle attaches). Ventrally, the second keeled intercentrum is pointed and the third intercentrum is wide and sutured between C2 and C3 (plate 4.2.1c).

3- C3-8

There are 8 cervical vertebrae (Hoffstetter and Gasc, 1969; Tilak, 1964), although El-Toubi (1945) observed 6. The neural spines of the presacral vertebrae are short with narrow tips and the first tall spine is that of C7 (where splenius capitis originates). The tips of C3-7 spines are rounded but become bilaterally compressed from C8 towards the dorsal region (spinalis/semispinalis complex). The posterior and anterior margins of the neural spines are smooth and curved. The vertebral centra are procoelous. As in Iguanidae*, the centra are long (C3-5), then become shorter (C6-8), and finally become long along the trunk region. The postzygapophyses are

smooth and horizontal. Ventrally, there are 4 smooth keeled intercentra, the first and second are larger than the third and fourth, which are small and round (plate 4.2.1e). Ventrally, the centra bear a midline keel between adjacent intercentra, after which the centra become wider (C6-8). The intercentra are sutured, and sometimes fused to the centrum behind (Islam, 1956; Tilak, 1964).

4- The anterior trunk vertebrae

The neural spines are longer and wider with a sharp anterior dorsal keel from D2 backwards. The tips of the neural spines are compressed (spinalis semispinalis muscle complex).

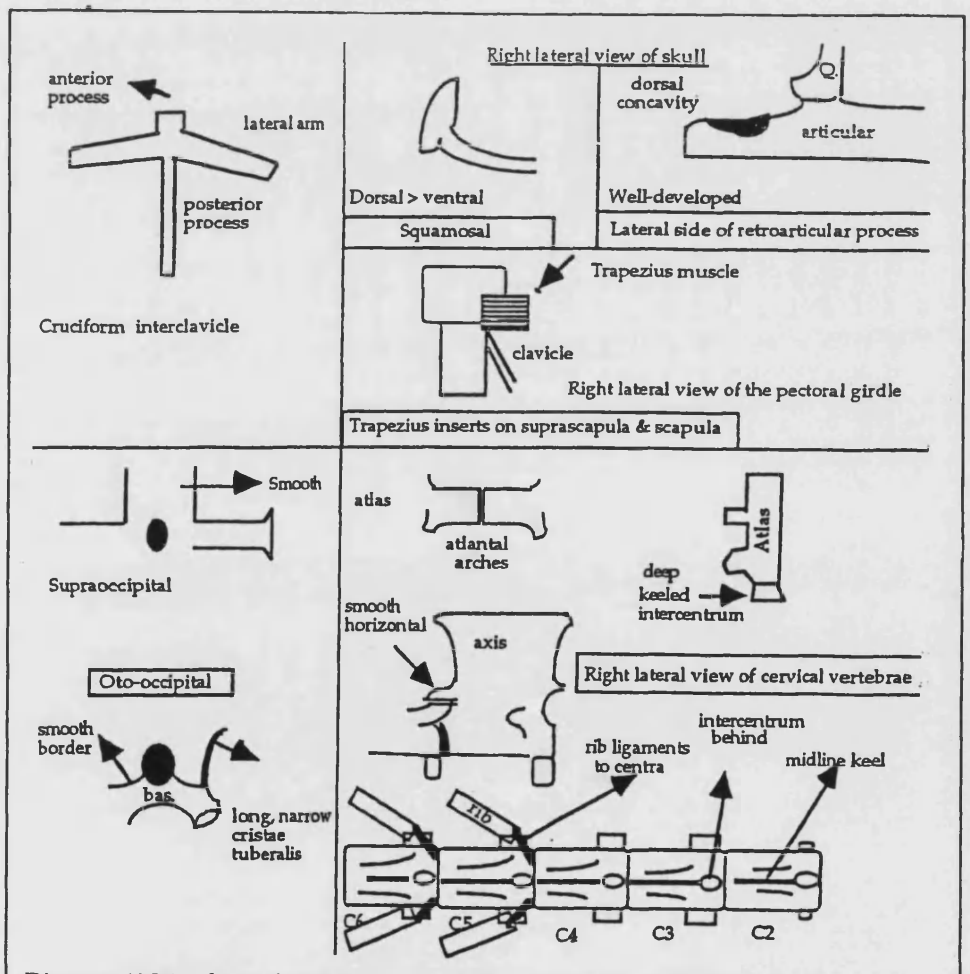


Diagram (4.2.1) of osteological craniocervical features in *U. aegyptia microlepis.*

5- Ribs

The rib ratio in *U. aegyptia* is 4+2+2 (plate 4.2.1d), as recorded by El-Toubi (1945, 1947), while Islam (1956) reported that the first cervical rib articulated on C3 in *Uromastyx hardwickii*. In *U. aegyptia*, the first cervical rib, which is on C5, possesses a wide distal end with a cartilage extension. The second cervical rib has a wide distal end, while the posterior cervical and trunk ribs are pointed (El-Toubi, 1945). The dorsal ribs are single headed and possess cartilaginous extensions. The rib ligaments connect the rib to the transverse process/centrum.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

It articulates with the suprascapula laterally.

3- Interclavicle

This cruciform bone has two short lateral arms, and the posterior stem is long and wide (Islam, 1956; El-Toubi, 1945; Tilak, 1964; Moody, 1980) (Fig., 4.2.1 a).

4- Scapulocoracoid and suprascapula

The well-developed scapula possesses a wide cartilaginous suprascapula dorsally, and has no direct attachment to the clavicle (Fig., 4.2.1 b).

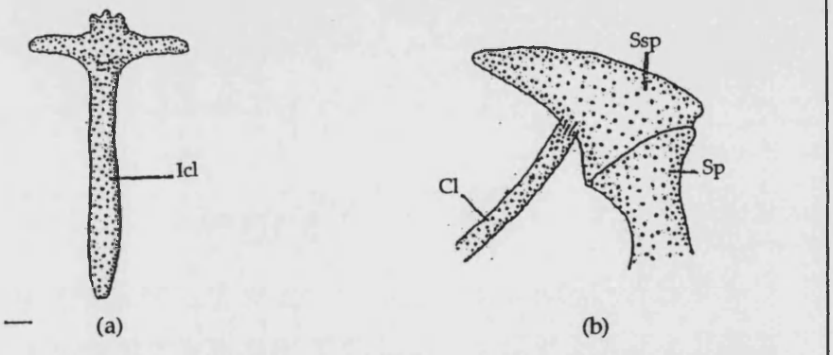


Fig. (4.2.1) *U. aegyptia microlepis*, a) Ventral view of the cruciform interclavicle (Icl); b) left lateral view of the pectoral girdle showing the clavicle (Cl) articulating with the suprascapula (Ssp). Sp = Scapulacoracoid. Scale bar = 1 mm.

Muscles of *Uromastyx aegyptia microlepis* (juvenile)

(Plate 4.2.2 – 4.2.3 – 4.2.4)

Superficial muscles

1- Depressor mandibulae internus and externus

The internus branch originates from the quadrate + supratemporal, while the externus branch originates from the supratemporal, squamosal, parietal and muscle fascia. The two muscles run as separate bundles and insert (overlapping each other) on the retroarticular process.

2- Cervicomandibularis

As in Iguanidae*, the muscle originates dorsally from the muscle fascia close to the parietal.

3, 4- Constrictor colli and latissimus dorsi

See chapter 1.

5- Trapezius

Originates from mid-dorsal line (4.2.2a), and inserts on the suprascapula close to its junction with the clavicle.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arm of the Interclavicle (Fig., 4.2.2), and inserts on the lateral edge of the paroccipital process (plate 4.2.3b).

Fig. (4.2.2) *U. aegyptia microlepis*, ventral view of the pectoral girdle showing the origin of the episternocleidomastoid (Ecm) from the interclavicle (Icl). Scale bar = 1 mm.

2- Clavicle dorsalis

Originates from the dorsal muscle fascia of longissimus capitis (plate 4.2.2c), and inserts on the anterolateral side of the clavicle (plate 4.2.3c).

3- Levator scapula dorsalis and ventralis and rib to suprascapula muscles

As in Iguanidae*.

4) Ribs to suprascapula muscle slips

There are first, second and third cervical rib muscle slips to the suprascapula dorsally. The third and fourth cervical rib muscle slips insert on the suprascapula /scapula posteriorly. The second cervical rib has a deep muscle slip to the suprascapula.

Deep muscles

1- Obliquus capitis

Originates from the anterior cervical spines (C2), and extends anteriorly (one layer) to insert on the dorsal and ventrolateral sides of the paroccipital process.

2- Rectus capitis

As in Iguanidae*.

3- Splenius capitis

Originates from the neural spines of C7-D3 (plate 4.2.4a), then extends anteriorly (single bundle) without branching to insert on the parietal (Khalil et al., 1977 - *Uromastyx;* Wahba et al., 1992a).

4- Spinalis muscles

a) Spinalis capitis

Absent.

B,c) Spinalis /semispinalis cervicus, Spinalis /semispinalis complex

See chapter 1.

5- Longissimus muscles

a, b) Longissimus dorsi, Longissimus cervicus

See chapter 1.

c) Longissimus capitis 1

Branches anteriorly from longissimus dorsi along C3, and inserts on the dorsolateral side of the parietal.

d) Longissimus capitis 2

Branches anteriorly deep from longissimus dorsi to insert (in an L-shape) on the lateral side of the paroccipital process.

e) Longissimus capitis 3

Absent.

f) Longissimus capitis 4

Branches laterally from longissimus dorsi to insert on the dorsolateral side of the basal tubera, and sometimes towards the ventrolateral tip of the oto-occipital (adult).

g) Longissimus capitis minor

The muscle starts along the C1 posterior process, and runs with the longissimus capitis 4 to insert on the basal tubera of the basioccipital.

6- Iliocostalis muscles

a, b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from the C7 centrum and C8 rib ligaments as tendinous bundles (plate 4.2.4b). The muscle extends anteriorly in two parts as fleshy bundles (starting from the centra/rib ligaments and intercentra) which then become tendinous along C2~3. The muscle finally inserts on the basal tubera.

b) Longus cervicus

Originates from C6 rib ligament, and extends anteriorly with slips from the cervical centra and rib ligaments to insert as one head on the second intercentrum (plate 4.2.4c).

8- First intercentral muscle slip to basioccipital and oto-occipital (superficial and deep)

Originates from the first keeled intercentrum such that the superficial branch ends on the central area of the basioccipital ventrally, while the deep branch ends dorsally on the concave ventrolateral surface of the oto-occipital near the crista tuberalis and the basioccipital.

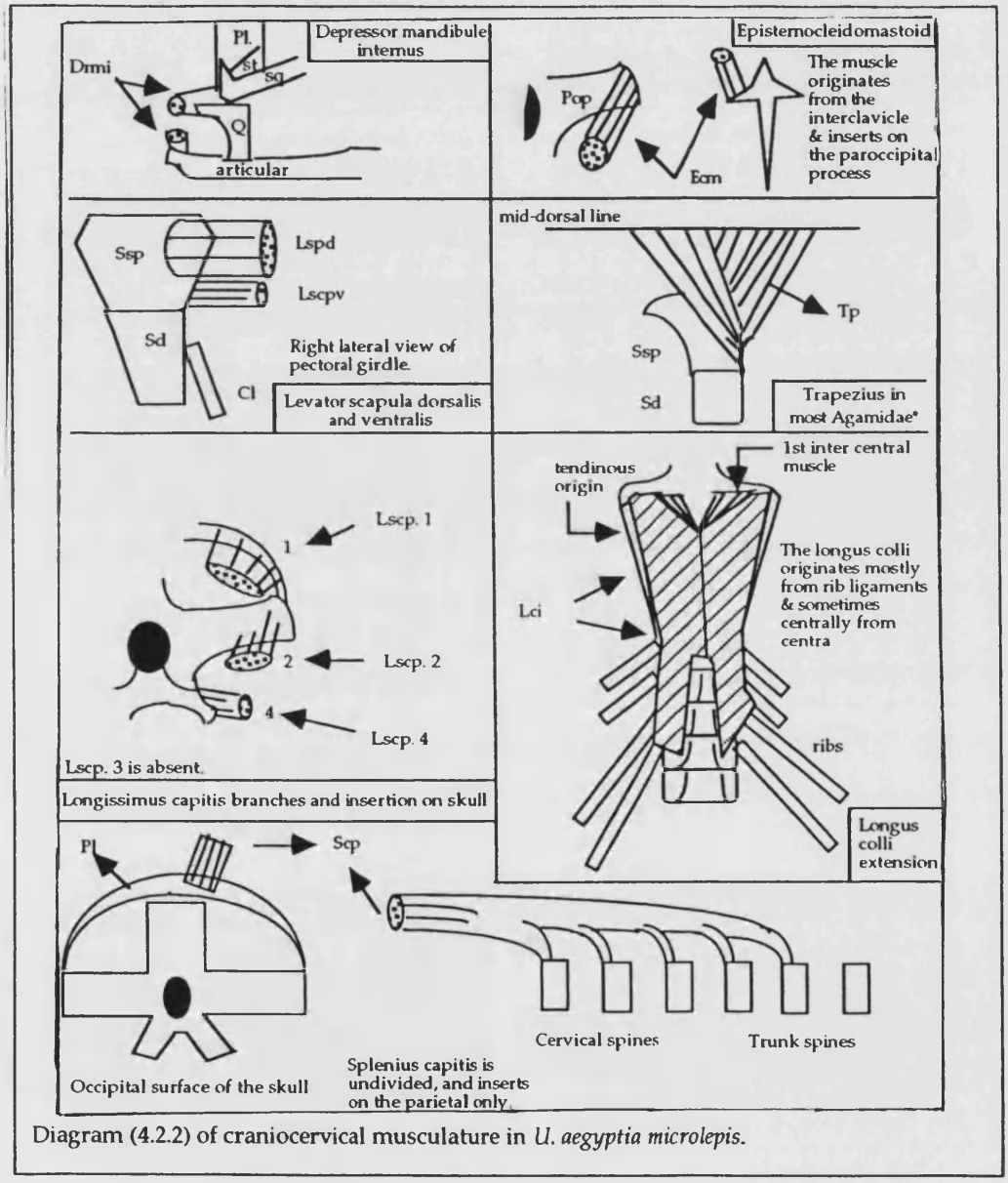


Diagram (4.2.2) of craniocervical musculature in *U. aegyptia microlepis*.

9- Posterior (2-3) intercentral muscle slips to basioccipital and oto-occipital

Ventrally, the muscles originate from the second and third intercentra, and insert broadly deep to longus colli on the basioccipital and on the

ventrolateral margin of the oto-occipital near the cristae tuberalis. The muscles insert partially superficial and lateral to the first (deep) intercentral muscle slip (as in Iguanidae*).

Very deep muscles

1- Deep oblique intercentra to rib ligaments

Originate from the second and third intercentra, and insert on the C4-5 rib ligaments (= iliocostalis muscle slips).

Comparison of osteological and muscular features within Agamidae*

A comparison of the neck anatomy between *Uromastyx aegyptia microlepis, Ceratophora stoddarti, Moloch horridus, Draco fimbriatus, Draco spilopteris* (skeleton), *Calotes versicolor, Phrynocephalus maculatus, Phrynocephalus mystaceus* (skeleton), *Agama agama, Pogona* sp., *Pogona barbata* (skeleton) shows similarities and variation (although some areas were not investigated in detail during dissection):

1) Similarities between agamids examined:

Excluding general similarities found in other lizards.

- Squamosal is usually divided posteriorly into dorsal + ventral processes. The dorsal process > the ventral process.
- Supratemporal extends along the parietal and paroccipital process.
- Supraoccipital midline ridge is absent.
- Intercentra are fused to centrum behind.
- Interclavicle is cruciform.
- Depressor mandibulae internus originates from quadrate and lateral skull components.
- Depressor mandibulae internus and externus run ventrally as two separate

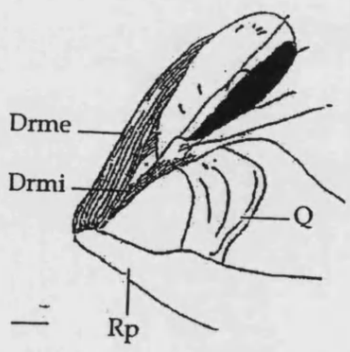


Fig. (4.2.3) *P. maculatus*, right lateral view of the posterior side of the skull showing the depressor mandibulae (Drme & Drmi) which runs as two separate bundles. Scale bar = 1 mm.

bundles to insert on the retroarticular process (Fig., 4.2.3).

- Splenius capitis originates centrally from neural spines.
- Longissimus capitis 4 inserts on the basioccipital and oto-occipital.
- Longissimus capitis minor runs parallel to longissimus capitis 4 and inserts on the basal tubera and oto-occipital
- Longus colli originates from centra +/- rib ligament and extends anteriorly in two parts.

<u>2) Variation between agamids examined</u>:

(Plate 4.2.5 – 4.2.6)

- The number of intercentra varies from 2 (*M. horridus*) (plate4.2.6c); 4 (*Uromastyx*); 5 (*C. stoddarti*); 6 (*C. versicolor, P. maculatus, A. agama, Pogona* sp.); and 7 (*D. fimbriatus*). The intercentra are fused to the centrum behind (4.2.6a), except in *Uromastyx* (juvenile) where they are sutured.
- The first cervical rib is on C5 except in *C. stoddarti* (C4) and in *D. fimbriatus* (C6). The rib ratio is usually but 4 + 2 + 2, in *C. stoddarti* is 3 + 3 + 2 and in *D. fimbriatus*, 5 + 3. The higher number of intercentra (7) and the special rib ratio (5 ribless + 3 cervical ribs) could reflect the gliding habit of *Draco* (Evans, 1982).
- In all agamids examined I recorded that the clavicle articulates with the suprascapula, but Iyer (1943) reported an articulation with the scapula in some agamids such as *Calotes versicolor*.
- In *Pogona, Uromastyx, C. stoddarti* and *P. maculatus*, the depressor mandibulae externus originates from the lateral skull components + parietal + muscle fascia, while in *A. agama, M. horridus, D. fimbriatus* and *C. versicolor* it originates from the parietal + muscle fascia. The depressor mandibulae internus and externus overlap each other during insertion

on the retroarticular process (plate 4.2.5a), except *C. stoddarti* and *D. fimbriatus* where they run in series (Fig., 4.2.4).

- In *C. stoddarti, P. maculatus, M. horridus* and *C. versicolor,* the trapezius inserts on the scapula + suprascapula, but in *Uromastyx, A. agama,* and *P. barbata,* it inserts on the suprascapula only. In *D. fimbriatus* the muscle inserts on suprascapula, scapula and clavicle Fig. (4.2.5).

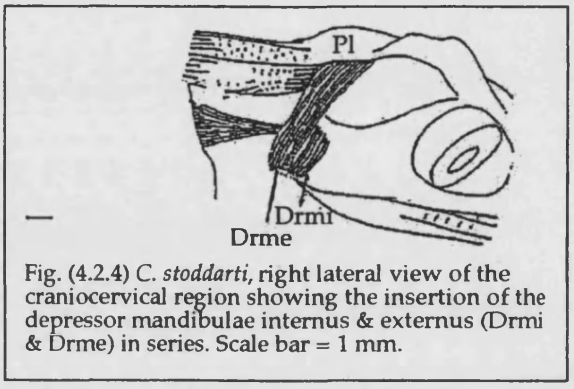
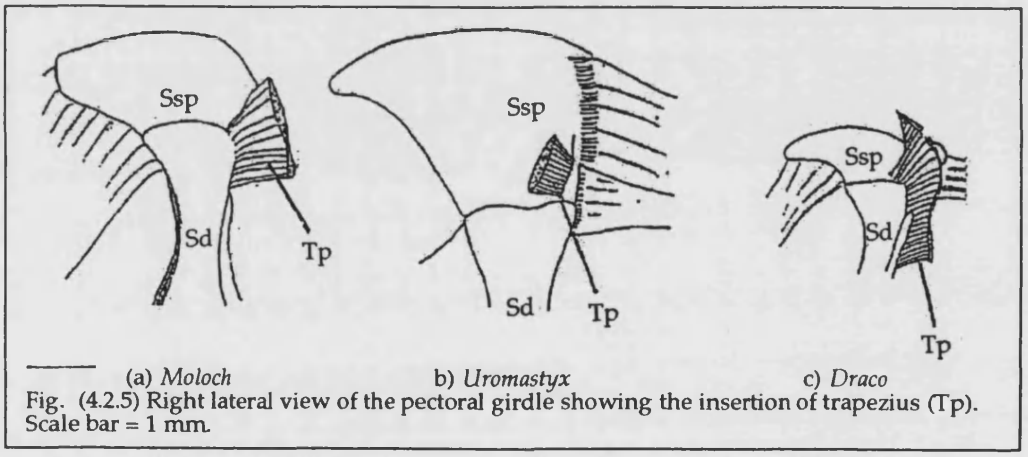


Fig. (4.2.4) *C. stoddarti,* right lateral view of the craniocervical region showing the insertion of the depressor mandibulae internus & externus (Drmi & Drme) in series. Scale bar = 1 mm.



(a) *Moloch* b) *Uromastyx* c) *Draco*

Fig. (4.2.5) Right lateral view of the pectoral girdle showing the insertion of trapezius (Tp). Scale bar = 1 mm.

- In all agamids examined, the episternocleidomastoid originates from the interclavicle, except in *Pogona* where it originates from the interclavicle + sternum (extra sternal head).
- Ribs to suprascapula/scapula muscle slips arise from the cervical ribs only (1-3 cervical ribs to suprascapula in *Uromastyx*; 1-4 cervical ribs to suprascapula in *Pogona, A. agama, P. maculatus* and *C. versicolor*; 1-5 cervical ribs to suprascapula in *C. stoddarti*), or from cervical and anterior trunk ribs (D1-3) (*M. horridus, D. fimbriatus*) (plate 4.2.5c).

- The longus colli originates from the dorsal vertebrae (*D. fimbriatus* and *M. horridus* = D3; *A. agama* = D2; *Pogona, C. versicolor* = D1), or from cervical vertebrae only (*P. maculatus* = C8; *C. stoddarti* = C7 [plate 4.2.6b]). Usually, the muscle begins from the centra and rib ligaments, except in *M. horridus* (centra) and *D. fimbriatus* where it arises from rib ligaments only.
- The longus cervicus begins from the dorsal vertebrae (*Moloch, Draco, Agama, D. fimbriatus, Pogona* = D2; *C. versicolor* = D1), or from the cervical vertebrae (*Uromastyx* = C6; *C. stoddarti* = C7; *P. maculatus* = C8). The muscle usually begins from the centra and rib ligaments, except in *D. fimbriatus* and *C. stoddarti,* where it begins from rib ligaments, and *M. horridus,* where it arises from centra only. Longus cervicus is usually equal in length to longus colli, but in *Uromastyx, D. fimbriatus* and *C. stoddarti,* the longus cervicus is shorter than longus colli.
- The posterior intercentral muscle slips to skull insert on the basioccipital + oto-occipital, except in *A. agama* where they insert on the oto-occipital. There may be one posterior intercentral muscle (*C. versicolor* [plate 4.2.6 d], *M. horridus*), two (*Uromastyx, A. agama*), three (*C. stoddarti, P. maculatus, Pogona sp.*), or five (*D. fimbriatus*) (plate 4.2.6e).
- In some agamids examined the cervical and trunk central tendon is present, but not in *Uromastyx, C. stoddarti, M. horridus* or *P. maculatus.*

Anatomy of the neck region in Chamaeleonidae

Four species of the genus *Chamaeleo* were dissected: *Chamaeleo jacksonii, Chamaeleo chamaeleon, Chamaeleo vulgaris* and *Chamaeleo dilepis,* but one species, *C. chamaeleon*, (+ *C. vulgaris* [skeleton]) was examined in more detail.

Previous works:

Baur, 1886; Siebenrock, 1893; Broom, 1925; Bellairs, 1969; Hoffstetter and Gasc, 1969; Rieppel, 1981; Estes et al., 1988; Frost and Etheridge, 1989; Rieppel and Crumly, 1997; Wahba et al, 1992b; Necas, 1999.

Osteology of *Chamaeleo chamaeleon*

(Plate 4.3.1)

Skull

1- Parietal

Dorsally, this is a rod-shaped bone that is wide anteriorly and forms a high casque up to several centimetres (plate 4.3.1b) (Necas, 1999). Ventrally, it contacts the supraoccipital by the crista parietalis inferior (where splenius capitis inserts). The bone lacks posterolateral processes. The squamosal runs instead to meet the parietal posterodorsally (Rieppel and Crumly, 1997).

2- Squamosal

This is a wide triradiate bone (where the depressor mandibulae internus and externus originate) that extends dorsally to meet the posterior crest of the parietal (plate 4.3.1b) (Broom, 1925). It extends laterally to attach to the supratemporal posteriorly and the quadrate dorsally. The dorsal process is larger than the ventral process.

3- Supratemporal

This elongated bone has lost its connection to the parietal (Rieppel, 1981), and is located posterolaterally between the paroccipital process and squamosal (where depressor mandibulae externus originates) (plate 4.3.1a).

Ventrally, it rests on the quadrate. In *Brookesia*, Siebenrock (1893) reported a reduced supratemporal bone, which may be fused to the squamosal.

4- Quadrate

This elongated bone has a straight dorsal surface where the squamosal, supratemporal and paroccipital process rest. The posterior margin is straight (where depressor mandibulae internus originates).

5- Retroarticular process

The retroarticular process is reduced (Estes et al., 1988) but retains a wide posterior end. The concavity is located internally (where depressor mandibulae internus and externus insert) (Fig., 4.3.1).

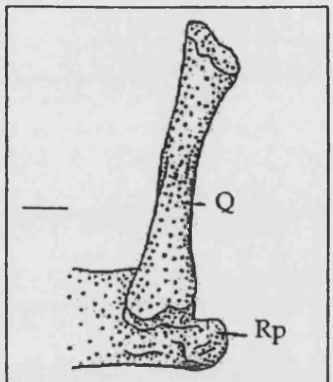


Fig. (4.3.1) *C. chamaeleon*, left lateral view of the quadrate (Q) and reduced retroarticular process (Rp). Scale bar = 1 mm.

6- Supraoccipital

The bone contacts the crista parietalis inferior anteriorly. Superiorly, it has a sharp keeled midline ridge to which the sharp crista parietalis inferior is fused (where splenius capitis, longissimus capitis 1 and 2 insert) (plate 4.3.1a).

7- Oto-occipital

The paroccipital process is wide and possesses a concave surface superiorly (where longissimus capitis 2 and 3 insert). The ventrolateral margin of the oto-occipital has a crista tuberalis (towards which longissimus capitis 4 and minor extend laterally). The ventral end of the oto-occipital, at the border with the basioccipital, has a curved ridge (where part of the intercentral muscle slips insert) (plate 4.3.1a).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera each possess one oval epiphysis (where longus colli and longissimus capitis 4 insert).

Presacral vertebral column

1- Atlas

Laterally, the atlantal arches possess long posterior processes (for longissimus cervicus) which have a dorsal tubercle (for the spinalis cervicus muscle slips), and a wide transverse process (where the iliocostalis cervicus and levator scapula dorsalis and ventralis attach) (plate 4.3.1c). Anterior to the transverse process there are two shallow linear ridges: a vertical dorsal one (where the atlas to paroccipital process muscle originates), and a horizontal ventral one (where the atlas to oto-occipital muscle - close to basal tubera~longissimus capitis minor originates). Ventrally, the intercentrum is deeply keeled. Baur (1886), described a pair of bony elements as a "proatlas" but my studies do not support this.

2- Axis

The posterodorsal process is oval. The axis postzygapophysis possesses tubercles (spinalis cervicus), and the articulation with the C3 prezygapophysis is horizontal. Ventrally, the axis centrum possesses a smooth deep second intercentrum and a third keeled intercentrum, which is sutured between C2 and C3 (plate 4.3.4b).

3- C3-5

There are 5 cervical vertebrae (Hoffstetter and Gasc, 1969; Estes et al., 1988; Necas, 1999) and 5 keeled intercentra (plate 4.3.1c). The neural spines of the five cervical vertebrae are long and vertical with narrow ends and compressed tips. The first tall neural spine is C4, and the spines increase in height posteriorly. The anterior and posterior margins of the neural spines

are straight and smooth. The length and the width of the arches are equal in C3, but the width becomes greater than the length in C4-5.

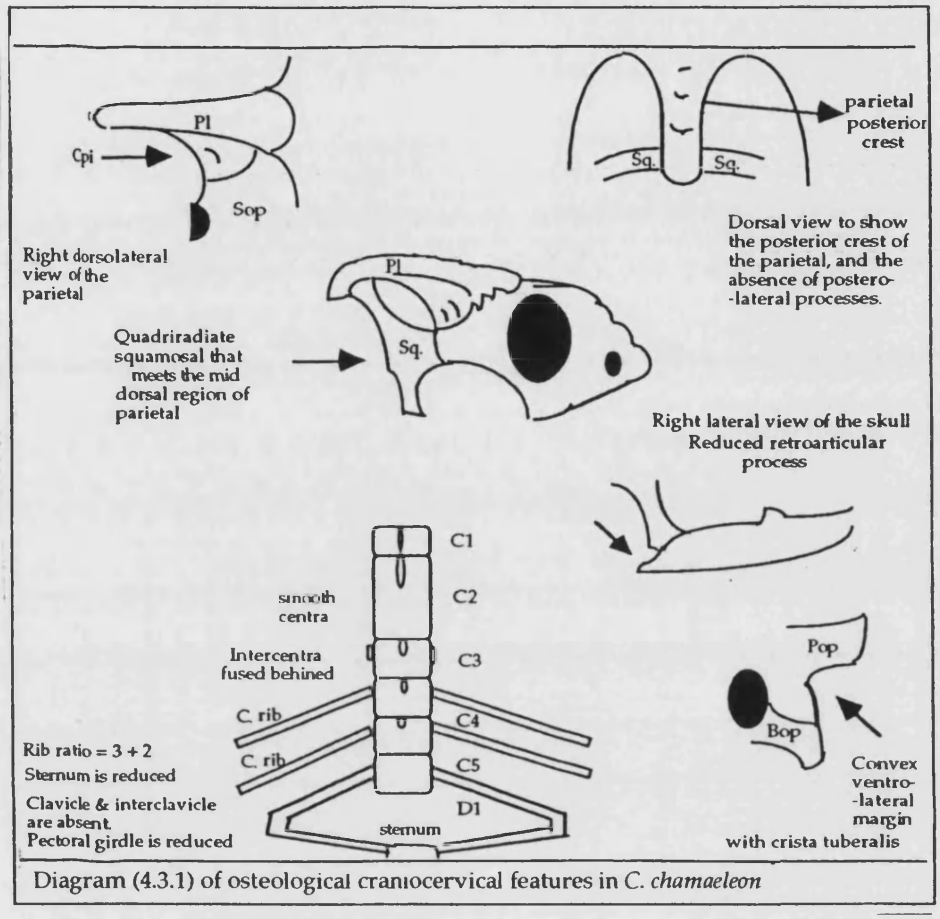


Diagram (4.3.1) of osteological craniocervical features in *C. chamaeleon*

The postzygapophyses are smooth and horizontal on C2-4, then become slightly inclined on C5 and continue this way towards D3, returning to the horizontal at D4. The vertebral centra are procoelous.

Ventrally, there are five smooth keeled intercentra along the five cervical vertebrae. The first four are deep and large, while the fifth is small and rounded. The intercentra are usually sutured and have an intervertebral position. A mid-central keel runs along C3-4, but the surface begins to be rounded towards C5 – D3 and becomes wider posteriorly along the dorsal vertebrae.

4- The anterior trunk vertebrae

The neural spines of the dorsal vertebrae are tall and long with a narrow dorsal margin and compressed tips. Laterally, the vertebral spines are biconcave from D2 towards the trunk region. Ventrally, the vertebral centra are wide and intercentra are absent.

5- Ribs

The rib ratio = 3 + 2 (plate 4.3.1c). There are two long narrow rounded free ribs on C4 and C5 (Rieppel, 1981). The distal end of the cervical ribs is narrow. There are no ligaments connecting the intercentra to the transverse process/rib area.

Pectoral girdle

1- Sternum

This is a small rectangular cartilaginous plate (where the episternocleidomastoid muscle originates) (plate 4.3.1d).

2- Clavicle

The bone is absent (may be short and fused to the anterior edge of the scapulocoracoid).

3- Interclavicle

Absent (Bellairs, 1969; Frost and Etheridge, 1998).

4- Scapulocoracoid and suprascapula

The coracoid is a wide bone without fenestrae, while the scapula is narrow and possesses a short wide suprascapula.

Muscles in *Chamaeleo chamaeleon*

(Plate 4.3.2 – 4.3.3)

Superficial muscles

1- Depressor mandibulae (internus and externus)

The depressor mandibulae internus originates mainly from the posterolateral margin of the quadrate + ventral edge of the squamosal, and

the externus branch originates dorsally from the dorsal edge of the quadrate + squamosal + supratemporal (plate 4.3.2b). The muscles insert on the retroarticular process in series (internus = anterior; externus = posterior).

2- Cervicomandibularis

Not identified during dissection (no attachment to muscle fascia, if present it originates from the squamosal only).

3- Constrictor colli

Not identified during dissection.

4- Trapezius

This short narrow muscle originates from the muscle fascia dorsally, and inserts on the anterior margin of the suprascapula (plate 4.3.2a). In *Chamaeleo parsonii* the muscle reportedly inserts on the scapula (Mivart, 1870).

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the anterior edge of the sternum (plate 4.3.1d), and inserts on the lower lateral side of the paroccipital process.

2- Clavicle dorsalis

Absent.

3- Levator scapula dorsalis and ventralis

See chapter 1.

4- Ribs to suprascapula and scapula muscles

The muscle slips originate from the C3 transverse process and the proximal end of the C4 rib, and insert on the superficial dorsal edge of the suprascapula. A deep muscle slip originates from the distal ends of the C4

and C5 ribs and inserts deep on the inner surface of the suprascapula. Posteriorly, a muscle originates from the very distal end of the C4 and C5 ribs to insert on the posterior margin of the scapula; one or more muscle slips originate from the distal ends of the C4, D1 and D2 ribs to insert on the posterior margin of the suprascapula/scapula.

Deep muscles

1- Obliquus capitis

Originates from C2-3 neural spines, and inserts on the dorsal surface of the paroccipital process.

2- Rectus capitis

Originates from C1 neural spine, and inserts on the dorsolateral edge of the supraoccipital.

3- Splenius capitis

Originates from C3-D1 neural spines centrally (plate 4.3.3b), and inserts anteriorly on the supraoccipital on the lateral side of the crista parietalis inferior (plate 4.3.2b).

4- Spinalis muscles

a) Spinalis capitis

Absent.

b, c) Spinalis/semispinalis cervicus, spinalis/ semispinalis complex

See chapter 1, also spinalis cervicus extends anteriorly to insert on the atlas posterior process.

5- Longissimus muscles

a, b) Longissimus dorsi and longissimus cervicus

See chapter 1.

c) Longissimus capitis 1

The muscle branches from longissimus dorsi along C4, and inserts on the supraoccipital (plate 4.3.2b) (lateral to the splenius capitis and superficial to the obliquus and rectus capitis).

d) Longissimus capitis 2

Branches from longissimus dorsi and along C3, and inserts on the dorsal side of the paroccipital process and supratemporal.

e) Longissimus capitis 3

Branches deep from longissimus dorsi and along C3, and inserts on the lateral side of the paroccipital process (plate 4.3.2c).

f) Atlas transverse process to paroccipital process muscle (dorsal branch)

Originates from the atlas transverse process (dorsal branch), and inserts on the ventral edge of the paroccipital process beside the longissimus capitis 3 (plate 4.3.2c, 4.3.4a). Its function is for extension and lateral rotation of the head (Wahba et al., 1992b). In humans, Clemente (1985), Agur et al. (1991), Warfel (1993) and Netter (1998) called this muscle the obliquus capitis superior.

g) Longissimus capitis 4

Branches ventrally along D1, and extends anteriorly to insert on the ventrolateral tip of the oto-occipital and the basal tubera.

h) Atlas transverse process to oto-occipital muscle (ventral branch) = Longissimus capitis minor

Originates from the atlas transverse process and extends with the longissimus capitis 4 to insert on the oto-occipital close to the basal tubera (plate 4.3.3a).

6- Iliocostalis muscles

a,b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from the anterior edge of D4 centrum (as muscle fibres) and extends anteriorly as a straight, thin, single bundle by originating from the centra and intercentra to insert on the basal tubera (with a tendinous bundle that begins along C4) (plate 4.3.3d).

b) Longus cervicus

Absent.

8- First intercentral muscle slip to basioccipital (superficial) and oto-occipital (deep)

Originates from the first intercentrum and extends anteriorly to insert on the central area between the basal tubera (superficial branch) and the oto-occipital (deep branch).

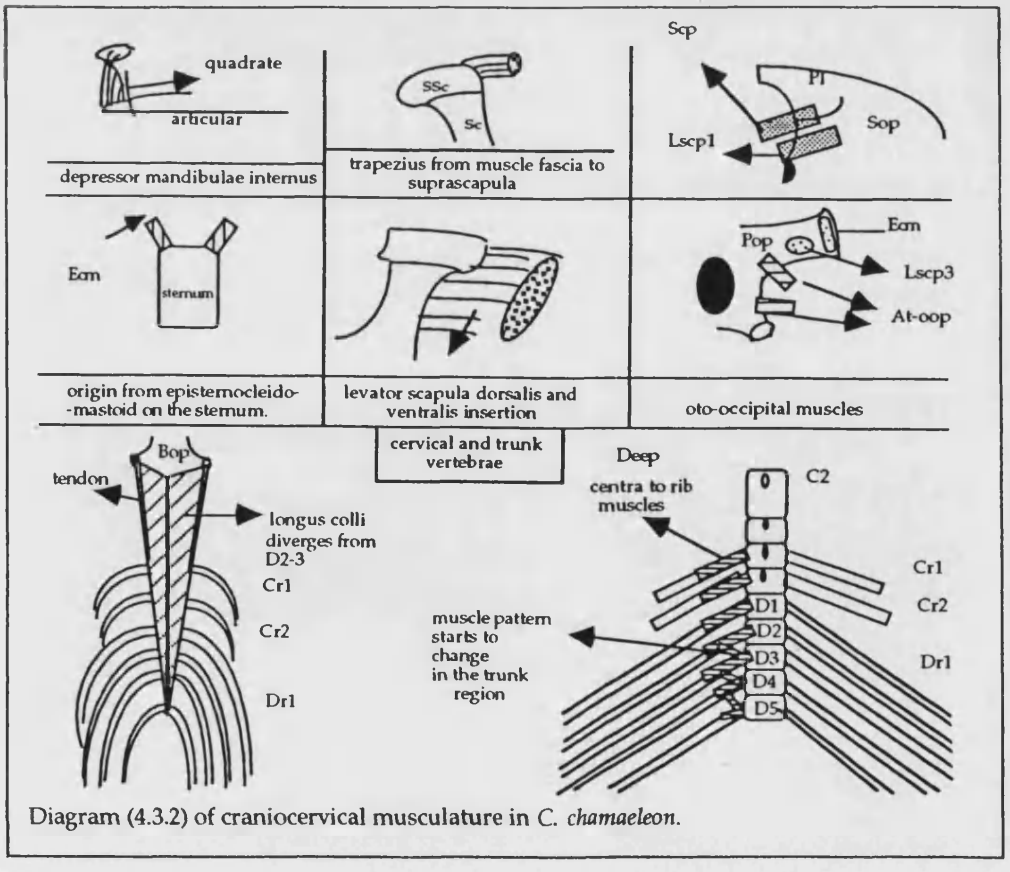


Diagram (4.3.2) of craniocervical musculature in *C. chamaeleon*.

9- Posterior (2-5) intercentral muscle slips to basioccipital and oto-occipital

Originate from 2nd – 5th intercentra, and extend anteriorly to insert on the basioccipital and cristae tuberalis of the oto-occipital (plate 4.3.3c). Ventrally, the posterior intercentral muscles insert deep to longus colli and partially superficial and lateral to the deep first intercentral muscle slip.

Very deep muscles

1- Intercentral / central muscle slips to adjacent ribs

The intercentra have long deep oblique muscle slips that insert on the adjacent rib shafts, such that 2nd – 4th intercentral muscles insert on the first cervical rib (C4 rib); and the fifth intercentral muscle inserts on the second cervical rib (C5 rib). The muscles continue along D1-2 centra and adjacent ribs, after which they disappear along the trunk region (plate 4.3.3d).

2- Cervical and trunk central tendon

Absent.

Comparison of osteological and muscular features within Chamaeleonidae

A comparison of the neck anatomy between *Chamaeleo jacksonii, Chamaeleo vulgaris, Chamaeleo dilepis* and *Chamaeleo chamaeleon* (dissected and skeletons) shows similarities and variation:

1) Similarities between examined chamaeleonids:

Excluding general similarities found in other lizards.

- Parietal lacks posterolateral processes and muscle attachment.
- Squamosal has an irregular triradiate shape.
- Supratemporal extends along the squamosal.
- Supraoccipital has a keeled midline ridge which is fused with the crista parietalis inferior.

- There are 5 cervical vertebrae. The dorsal ends of the spines become wide on C5 and continue like this to the dorsal region. The anterior and posterior margins of the neural spines are straight.
- Rib ratio 3 +2.
- Interclavicle and clavicle are absent.
- Sternum is compressed laterally (poorly developed).
- Depressor mandibulae internus and externus originate mainly from the quadrate and lateral skull components. Both muscles insert on the retroarticular process in series.
- Trapezius inserts on the suprascapula.
- Episternocleidomastoid originates from the sternum.
- Clavicle dorsalis is absent.
- Ribs to suprascapula muscle slips extend along the cervical and dorsal ribs.
- Third transverse process bears the first muscle slip to the dorsal suprascapula area.
- Splenius capitis originates centrally from the spine tips, and inserts on the supraoccipital.
- Spinalis cervicus has anterior branch to the atlas posterior process.
- Longissimus capitis 1 inserts on the supraoccipital.
- Longissimus capitis 2 inserts on the paroccipital process and lateral skull components.
- Longissimus capitis 3 is present.
- Longissimus capitis 4 inserts on the basioccipital and oto-occipital.
- Longissimus capitis minor (= atlas transverse process to oto-occipital) inserts on the oto-occipital close to the basal tubera.

- The atlas has a short dorsal muscle which originates from the transverse process and inserts on the paroccipital process.
- Longus colli originates from centra or intercentra, and extends centrally as a narrow muscle that diverges wide anteriorly.
- Longus cervicus is absent.
- Intercentral/central long lateral muscle slips to ribs are present, and extend uniformly along the cervical region only.

<u>2) Variation between examined chamaeleonids:</u>

(Plate 4.3.4)

- Supratemporal is present in all examined chamaeleonids, except C. *jacksonii* (plate 4.3.4a).
- Axis postzygapophysis is smooth (*Chamaeleo jacksonii, Chamaeleo vulgaris*), or possesses tubercles (*Chamaeleo chamaeleon, Chamaeleo dilepis*).
- The number of cervical intercentra ranges between 5 (C. *chamaeleon*), 4 (C. *dilepis*), 3 (C. *vulgaris*), and 2 (C. *jacksonii*). In C. *jacksonii*, C. *vulgaris* and C. *dilepis*, the centrum is smooth and the intercentra are fused to the centrum behind; in C. *chamaeleon*, the centrum is keeled between the intercentra, and the intercentra are sutured (plate 4.3.4b) (or placed towards the centrum behind).
- In C. *chamaeleon* and C. *dilepis*, there are cervical and dorsal ribs to posterior suprascapula muscle slips (plate 4.3.4c), but in C. *jacksonii* and C. *vulgaris* there are muscle slips from the cervical ribs.
- In most chamaeleonids examined the longissimus capitis 2 inserts on the paroccipital process, supratemporal and squamosal, except in C. *jacksonii* where it inserts on the dorsal process of the squamosal (the supratemporal is absent).

- Longus colli originates from D4 (*C. chamaeleon*); D3 (*C. vulgaris*); Posterior edge of D2 (*C. jacksonii* [plate 4.3.4d]); and the anterior edge of D2 (*C. dilepis*).
- In *C. chamaeleon*, there are 5 intercentral muscle slips to skull; 4 in *C. dilepis*; 3 in *C. vulgaris*; and 2 in *C. jacksonii* (Fig., 4.3.2).

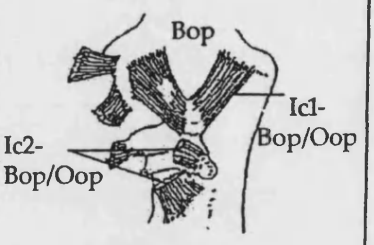


Fig. (4.3.2) *C. jacksonii*, ventral view of the craniocervical region showing intercentral muscle slips to skull (Ic[1-2]-Bop/Oop). Scale bar = 1 mm.

Comparison of osteological and muscular features within Iguania

Table (4.4a) Osteology

Family name / Bone features	Iguanidae*	Agamidae*	Chamaeleonidae
Position of intercentra	Mostly sutured or fused to the centrum in front	Fused to centrum behind	
Shape of interclavicle	T-shaped	Cruciform	Absent

Table (4.4b) Myology

Family name / Muscles features	Iguanidae*	Agamidae*	Chamaeleonidae
Origin of depressor mandibulae internus	Skull roof (parietal or squamosal)	Quadrate + lateral skull components	Quadrate + squamosal
Splenius capitis insertion	Parietal + supraoccipital	Parietal	Supraoccipital
Longissimus capitis 4 insertion	Basioccipital	Basioccipital + oto-occipital	
Longus colli origin	Midline and lateral heads (centra/intercentra and rib ligaments)		Midline only (centra/intercentra)
Longus colli extension	Two layers		One layer

Common craniocervical features in Iguania

Osteology

1- Squamosal has a dorsal process.

Myology

1- Deep ribs to suprascapula slips are present.

2- Longissimus capitis minor runs close and parallel to longissimus capitis 4 to insert on the basioccipital and oto-occipital.

3- Longus colli tendon of insertion is present.

4- First intercentral to skull muscle slip inserts on the basioccipital (superficial) and oto-occipital (deep).

5- Posterior intercentral muscle slips insert on the ventrolateral margin of the oto-occipital (convex edge), while longissimus capitis 4 and minor insert ventrally close to basioccipital.

6- Ventrally, the posterior intercentral muscles insert on the skull deeper to longus colli and superficial and lateral to the first (deep) intercentral muscle slip.

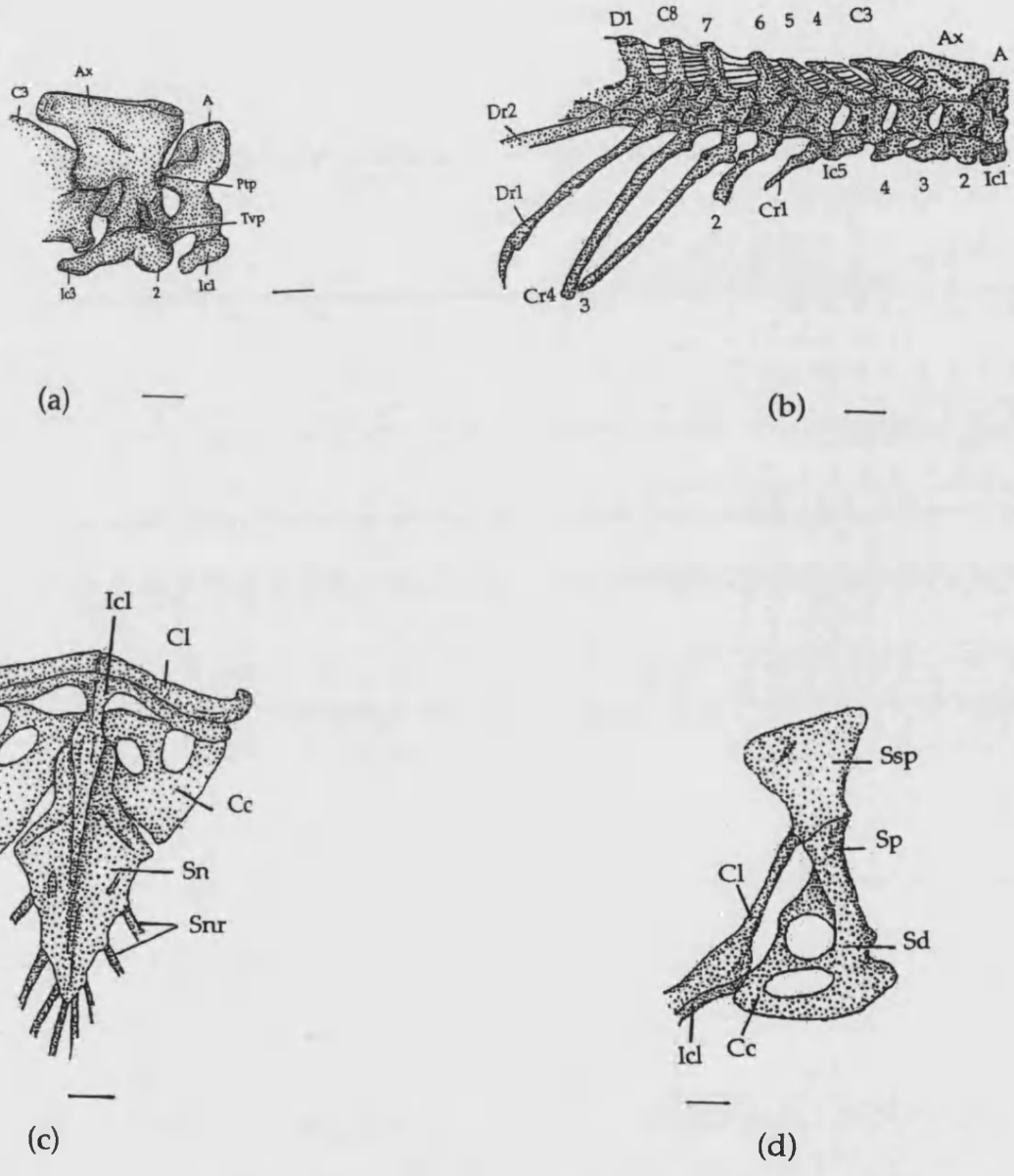


Plate (4.1.1) *Anolis edwardii,* a) right lateral view of the atlas/axis complex; b) right lateral view of the cervical vertebrae and anterior dorsal vertebrae with rib ratio 4+2+2; c) ventral view of the pectoral girdle, sternum (Sn), coracoid (Cc) with fenestrae, clavicle (Cl) and interclavicle (Icl); d) left lateral view of the pectoral girdle showing the suprascapula (Ssp), scapulocoracoid (Sd) and the clavicle (Cl). Axis = Ax; Atlas = A; Posterior process=Ptp; Transverse process = Tvp. Scale bar = 1 mm.

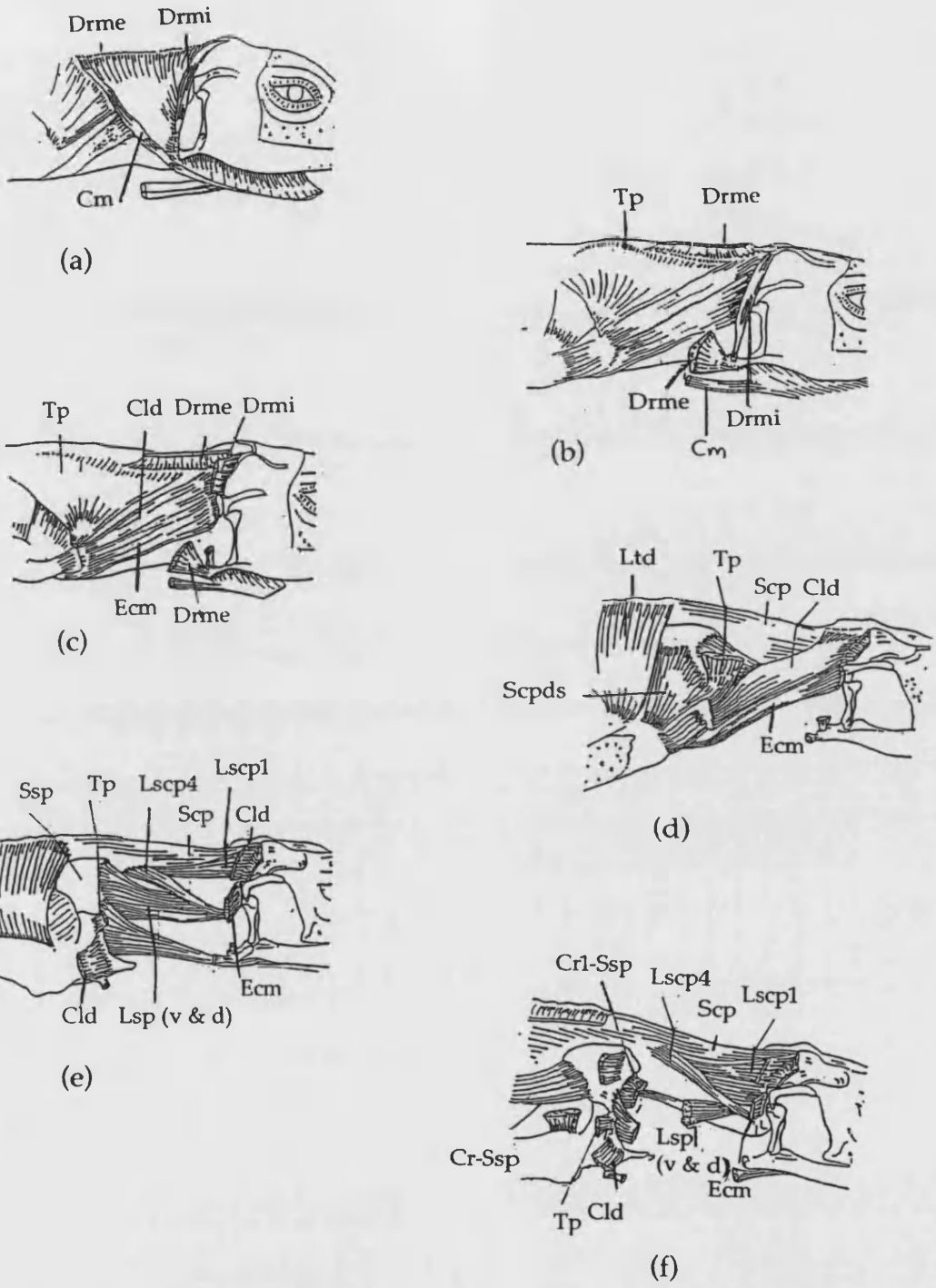


Plate (4.1.2) *Anolis richardii*, right lateral view of the craniocervical region, a) depressor mandibulae externus and internus (Drme & Drmi) and cervicomandibularis (Cm); b) origin and insertion of trapezius (Tp); c, d) clavicle dorsalis (Cld) and episternocleidomastoid (Ecm) origin and extension and splenius capitis (Scp); e) levator scapula dorsalis and ventralis (Lspv & Lspd), and extension of longissimus capitis 4 (Lscp4); f) longissimus capitis (Lscp) branches to the skull. Scale bar = 1 mm.

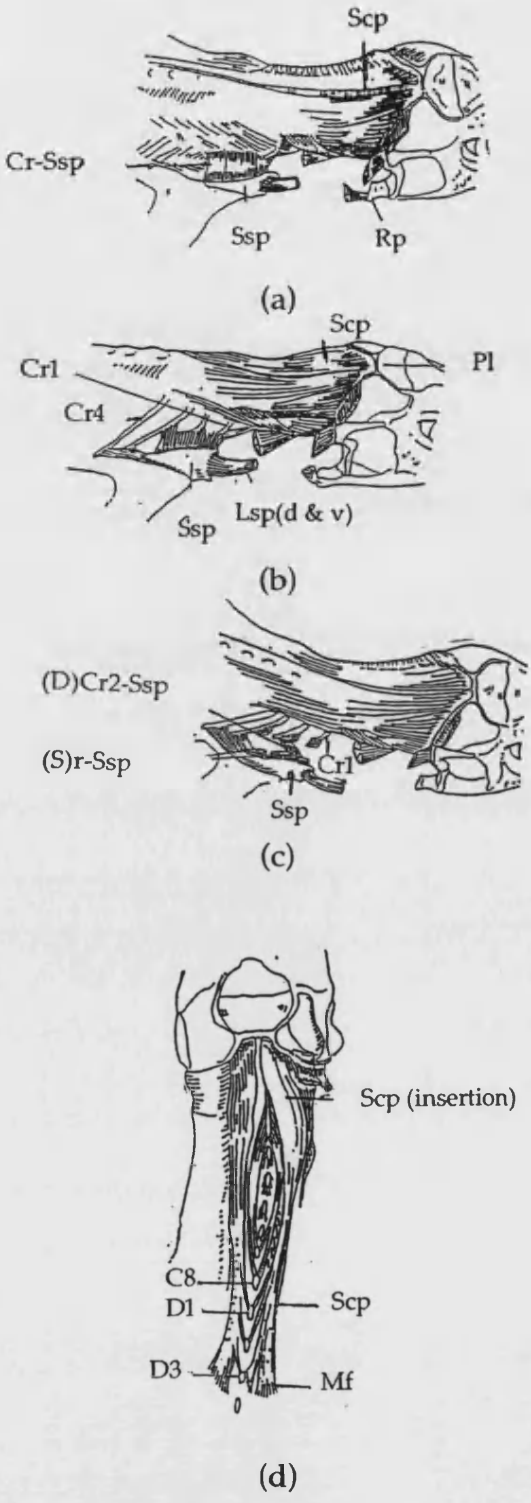
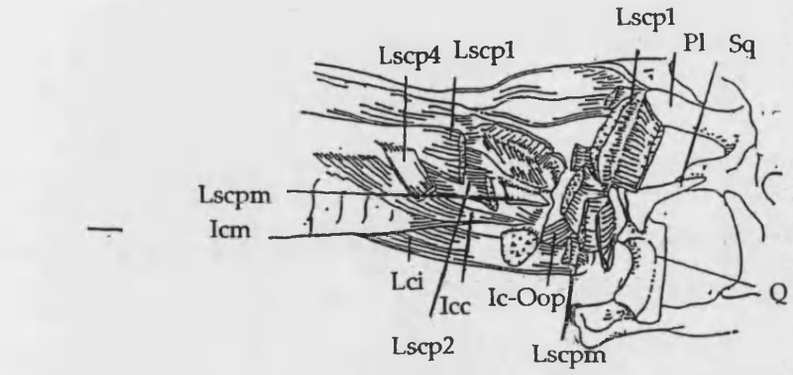
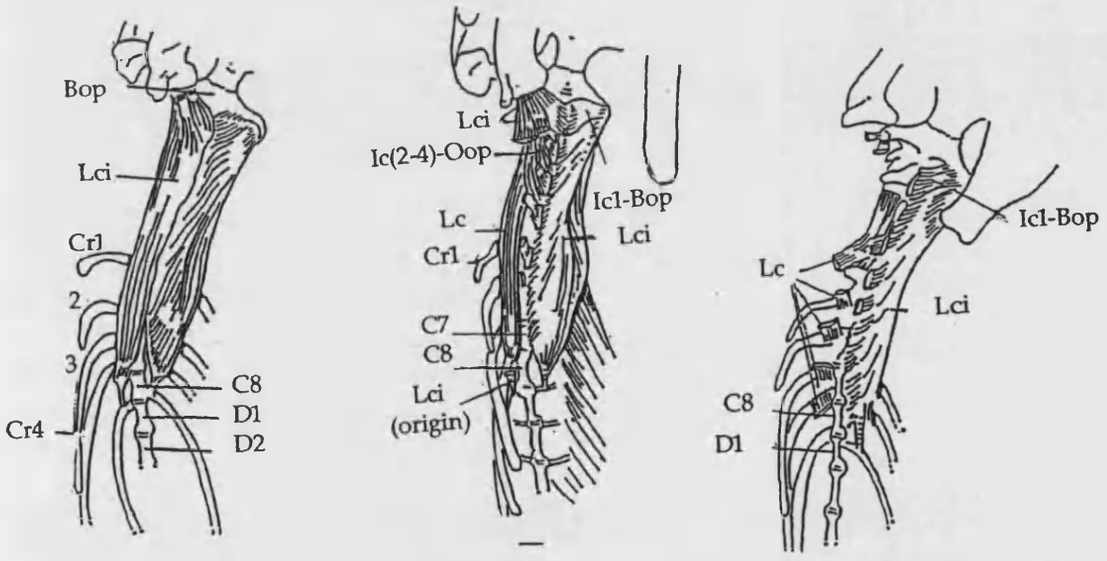


Plate (4.1.3) *Anolis richardii*, a, b, c) right dorsolateral view of the craniocervical region showing the origin, extension and insertion of cervical rib (superficial & deep) to suprascapula muscle slips (Cr & [D]Cr-Ssp). Dorsal view of the craniocervical region, d) origin of splenius capitis (Scp) from neural spines and muscle fascia. Scale bar = 1 mm.



(a)



(b) (c) (d)

Plate (4.1.4) *Anolis richardii*, a) right dorsolateral view of the craniocervical region showing the iliocostalis cervicus (Icc) insertion on the atlas transverse process, longus colli (Lci). Ventral view of the craniocervical region (b-d), b) longus colli (Lci) origin and insertion are seen (C8 and D1 rib ligament), c) longus colli is cut and longus cervicus (Lc) origin is visible (C8 rib ligament) and intercentral muscle slip (Ic1-4) insertion, d) longus cervicus muscle slips from rib ligaments (Rl) and final insertion on the axis intercentrum. Scale bar = 1 mm.

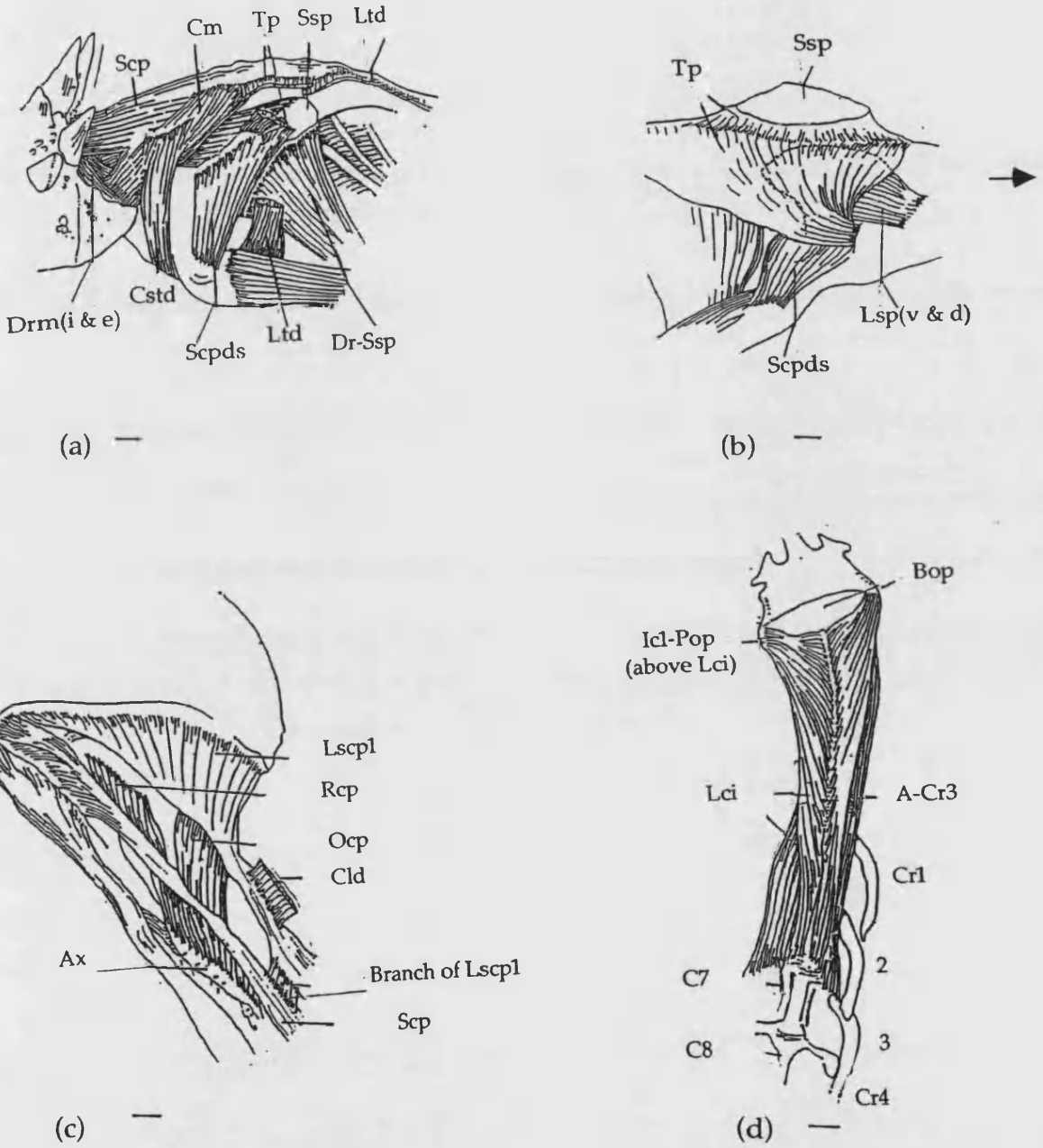
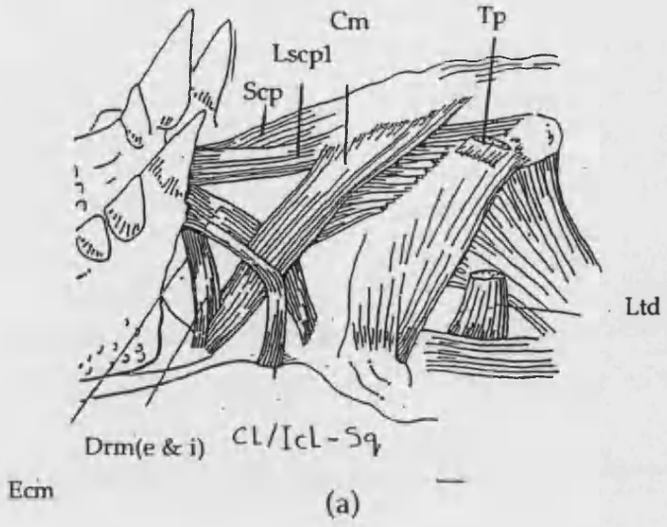


Plate (4.1.5) a) *Phrynosoma platyrhinos*; left lateral view of the craniocervical region showing constrictor colli (Cstc), trapezius (Tp) and cervicomandibularis (Cm); b) *Oplurus cyclurus*, right dorsolateral view of the trunk region showing the origin of trapezius (Tp) from mid-dorsal line (spine tips); c) *O. cyclurus*, left dorsal view of the craniocervical region showing the origin of clavicle dorsalis (Cld) from muscle fascia, anterior connection between longissimus capitis 1 (Lscp1) and splenius capitis (Scp); d) *Iguana iguana*, ventral view of the craniocervical region with atlas to 3rd cervical rib muscle (A-Cr3), both longus colli (Lci) and cervicus (Lsc) originate from the C6 and C7 rib ligament. Scale bar = 1 mm.



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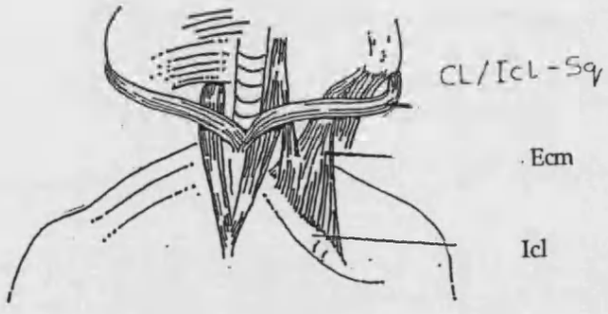

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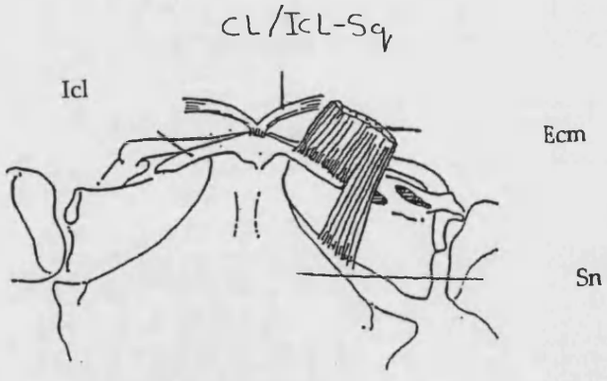


(c)

Plate (4.1.6) *Phrynosoma platyrhinos* a) left lateral view of the craniocervical region showing the clavicle/interclavicle muscle to squamosal (Cl/ Icl-Sq); b) ventral view where clavicle/ interclavicle muscle originates; c) ventral view of the pectoral girdle showing the origin of episternocleidomastoid (Ecm) from interclavicle (Icl) and sternum (Sn). Scale bar = 1 mm.

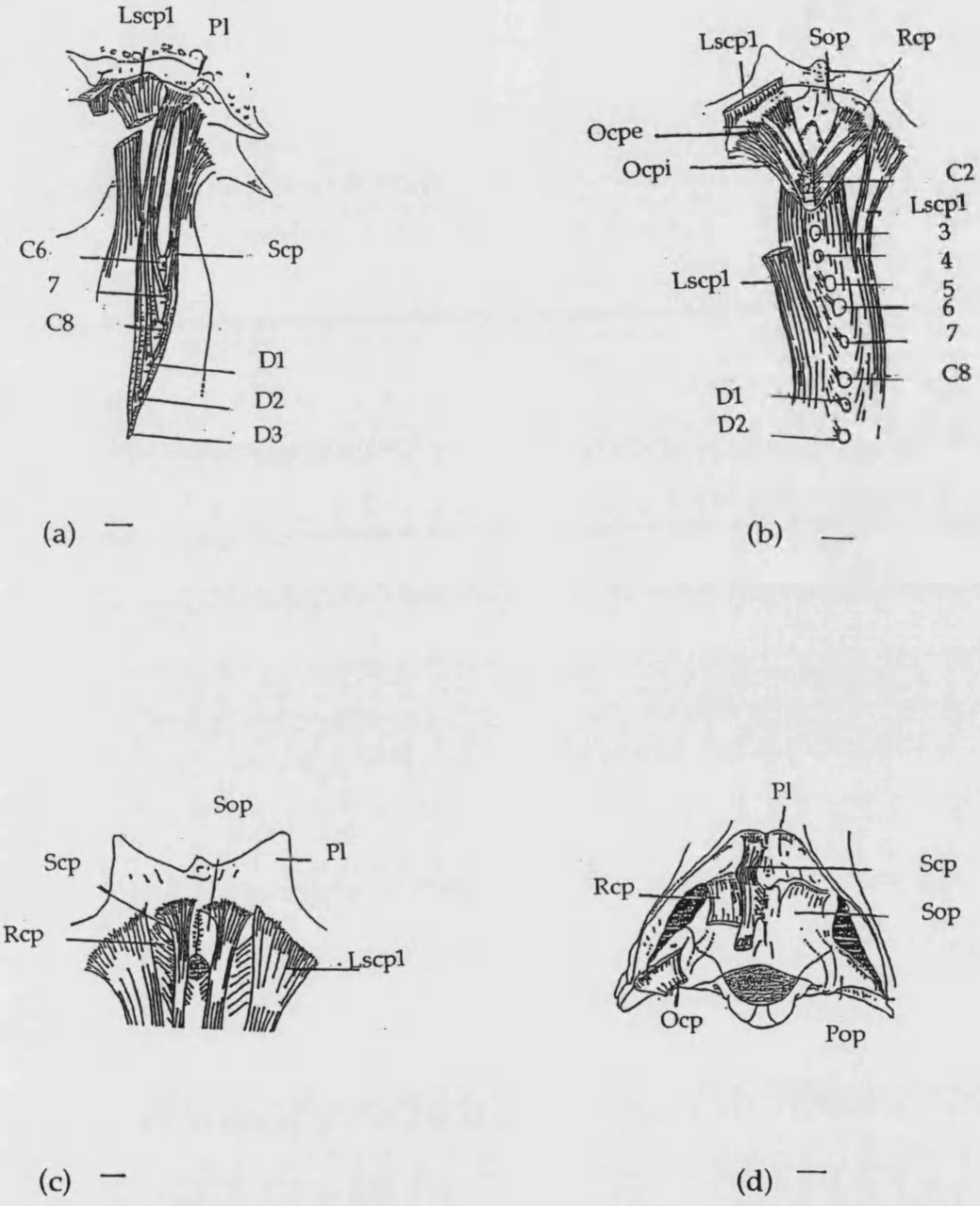
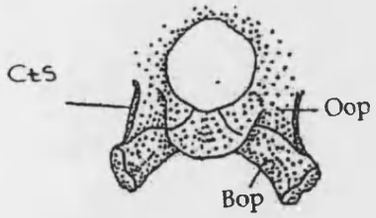


Plate (4.1.7) *Phrynosoma platyrhinos* a) dorsal view of the craniocervical region showing the origin of splenius capitis (Scp) from spines only; b) division of obliquus capitis (Ocp); c) posterior view of the skull showing the insertion of splenius capitis on parietal and supraoccipital. d) *Oplurus cyclurus*, posterodorsal posterior view of the skull showing the insertion of splenius capitis (Scp) on supraoccipital and parietal. Scale bar = 1 mm.



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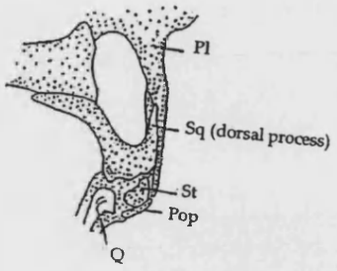

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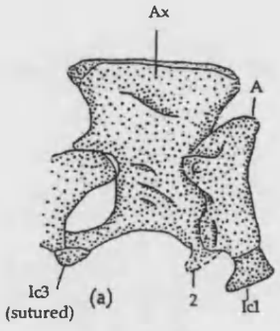

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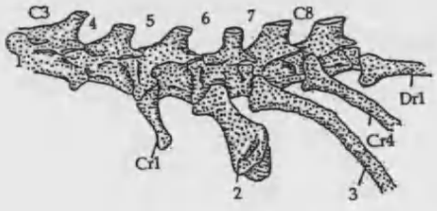

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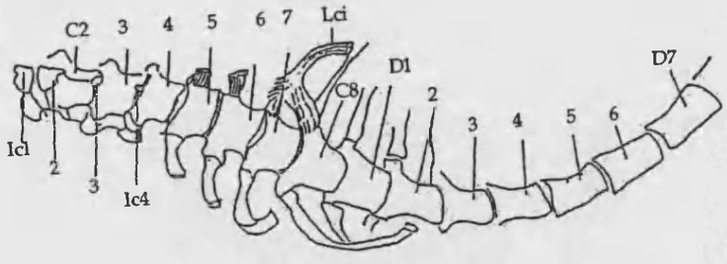
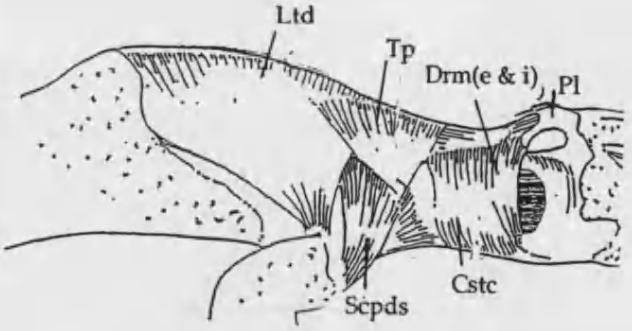


(e)

Plate (4.2.1) *Uromastyx aegyptia,* a) occipital view of the skull showing the crista tuberalis (Cts) on the ventrolateral margin of the oto-occipital (Oop); b) left lateral view of the skull showing the dorsal process of the squamosal (Sq); c) right lateral view of the atlas/axis complex with sutured 3rd intercentrum (Ic3); d) left lateral view of the cervical vertebrae where 4 cervical ribs (Cr4) articulate; e) left ventral view of the cervical and dorsal vertebrae with 4 small sutured intercentra (Ic1-4). Scale bar = 1 mm.



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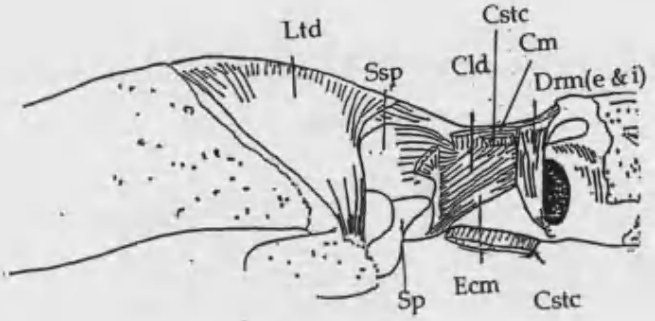

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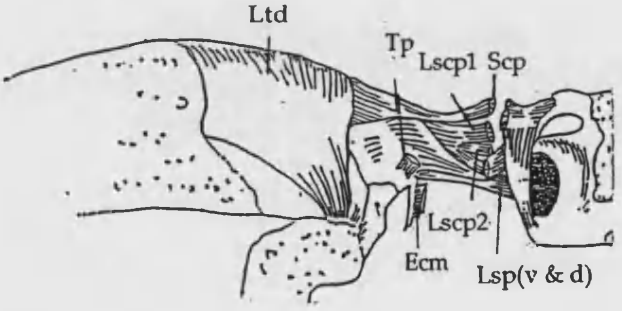

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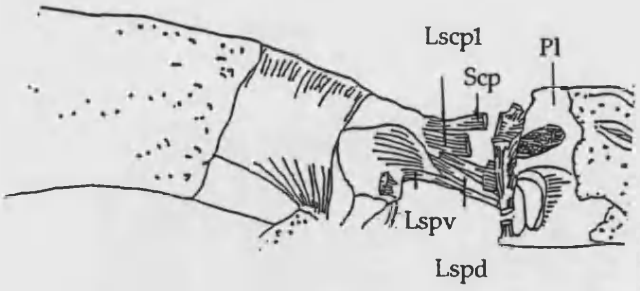
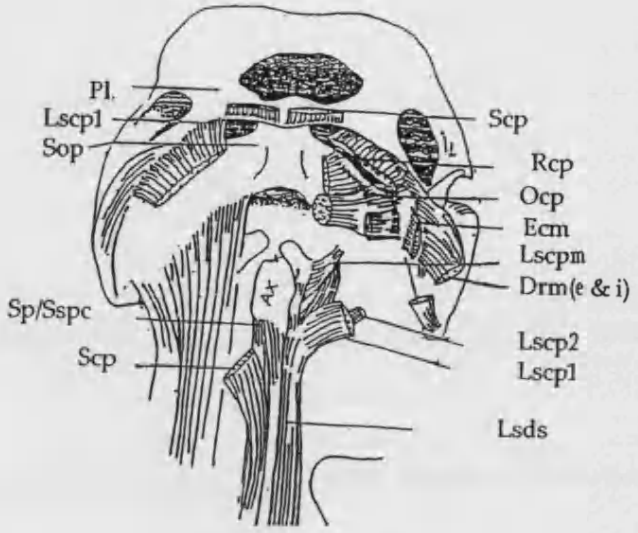


(d)

Plate (4.2.2) *Uromastyx aegyptia*, right lateral views of the craniocervical region from superficial to deep, a) constrictor colli (Cstc), trapezius (Tp) and latissimus dorsi (Ltd); b) depressor mandibulae (Drm), cervicomandibularis (Cm), clavicle dorsalis (Cld) and episternocleidomastoid (Ecm); c) longissimus capitis (Lscp) branches and splenius capitis (Scp); d) levator scapula dorsalis and ventralis (Lspd & Lspv). Scale bar = 1 mm.



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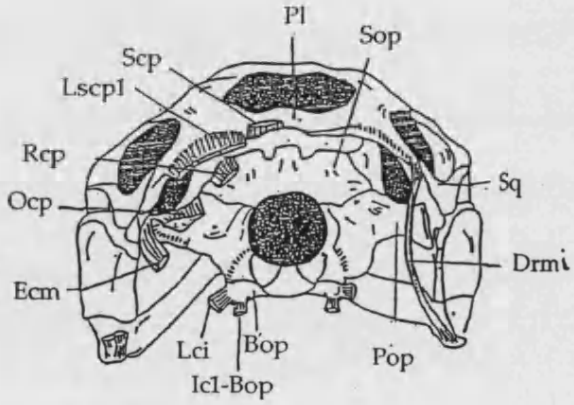

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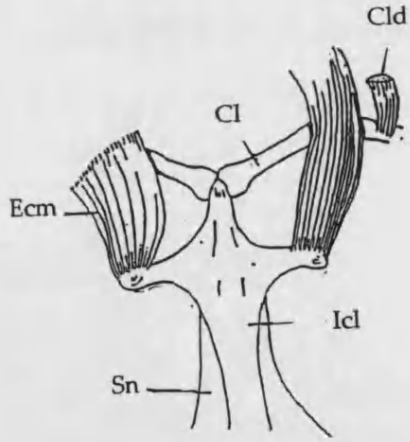


(c)

Plate (4.2.3) *Uromastyx aegyptia*, a) occipital view of the craniocervical region with most superficial, intermediate and deep muscles attaching on the skull and cervical vertebrae; b) occipital view of the skull with the attachment of most intermediate and deep muscles; c) ventral view of cruciform interclavicle (Icl) where episternocleidomastoid (Ecm) originates. Clavicle dorsalis (Cld), Depressor mandibulae externus & internus (Drm[e+i]), intercentral 1 to basioccipital (Ic1-Bop), longissimus capitis 1, 2&minor (Lscp1,2&m), Longissimus dorsi (Lsds), Obliquus & rectus capitis (Ocp & Rcp). Scale bar = 1 mm.

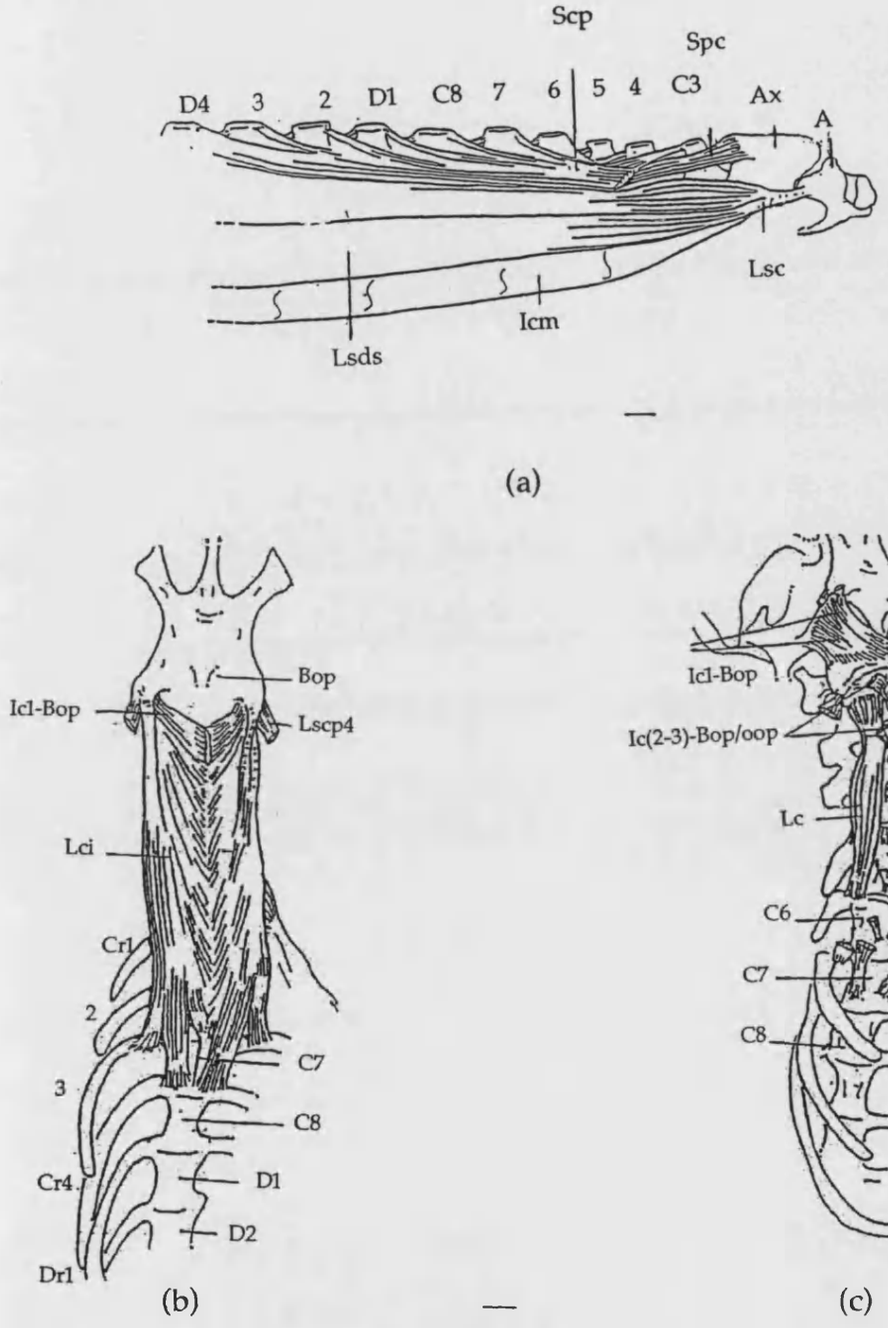
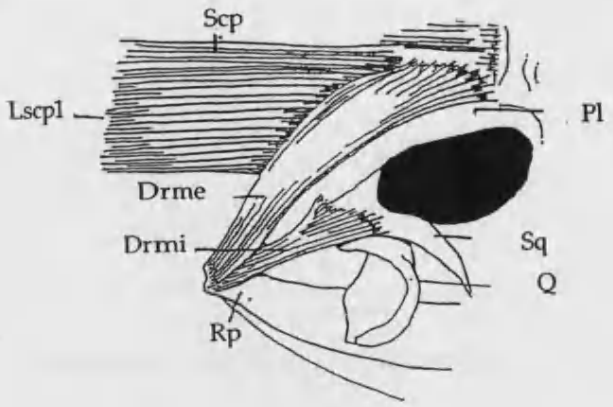


Plate (4.2.4) *Uromastyx aegyptia*, a) right lateral view of the cervical and dorsal vertebrae showing the origin of splenius capitis (Scp) from neural spines only, insertion of spinalis cervicus (Spc), insertion of iliocostalis major (Icm); b) ventral view of the craniocervical region showing the beginning of longus colli (Lci) from rib ligament and centrum (C7 / C8 centrum and rib ligaments); c) deep ventral view of the craniocervical region showing the longus cervicus (Lc) (C6) is shorter than longus colli (Lci) (C8). Scale bar = 1 mm.



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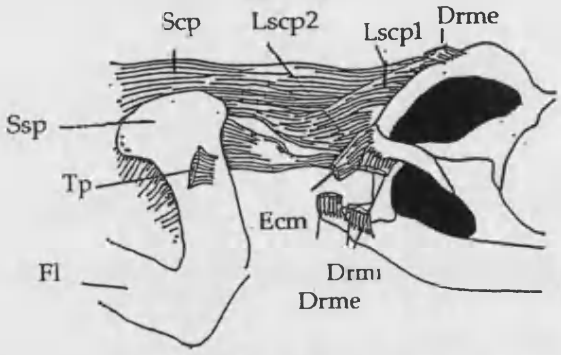

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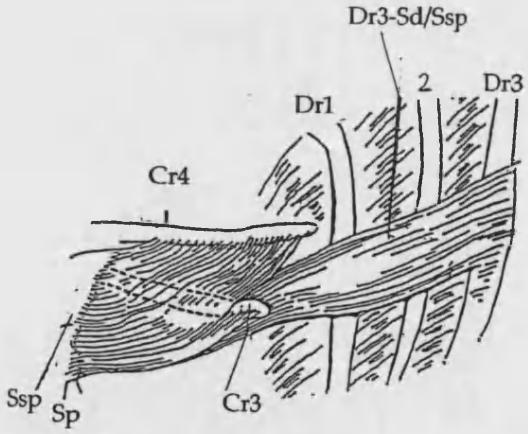
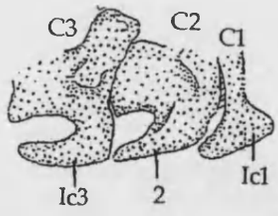


(c)

Plate (4.2.5) right lateral view, a-c, a) *Agama agama*;, division of depressor mandibulae internus and externus (Drmi & Drme). b) *Ceratophora stoddarti*; depressor mandibulae internus and externus insert in series. c) *Moloch horridus*, left lateral view of the ribs showing the origin of 3rd dorsal rib muscle slip which inserts on the scapulocoracoid/ suprascapula (Dr3-Sd/Ssp). Scale bar = 1 mm.



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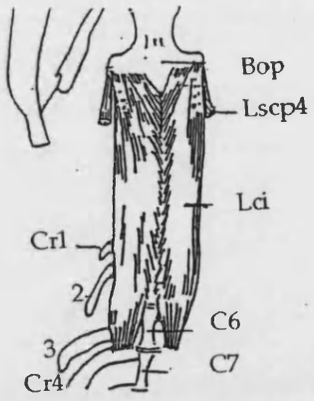

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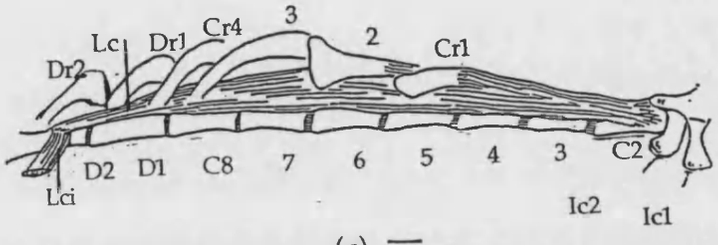

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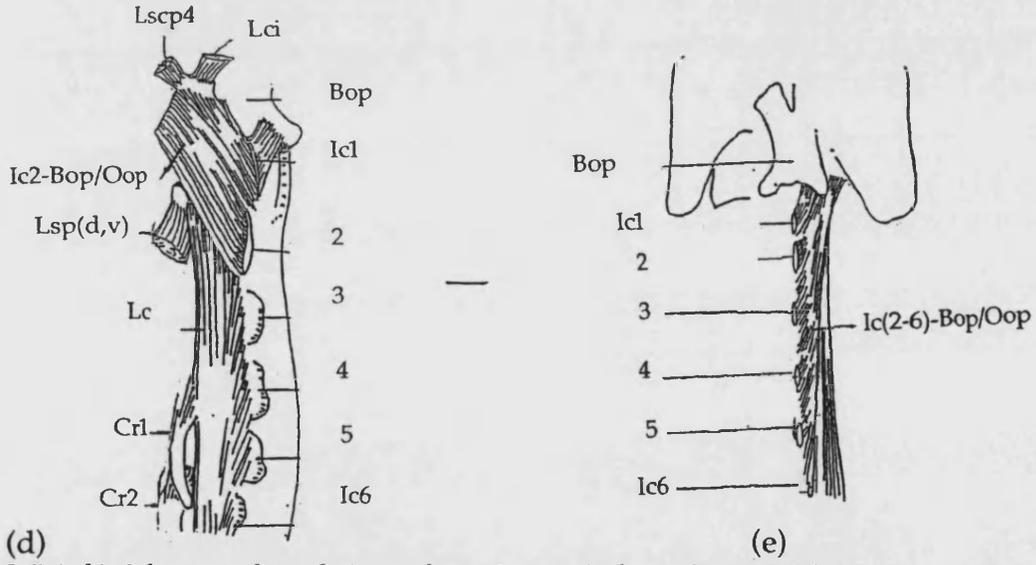
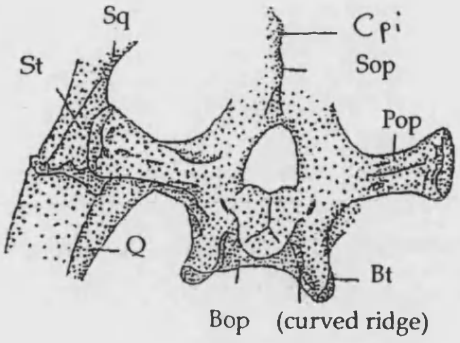


(d) (e)

Plate (4.2.6) (a-b) right ventrolateral views of anterior cervical vertebrae, a) *Calotes versicolor*, intercentra are fused to the centrum behind. b) *Crotaphytus stoddarti*, ventral view of craniocervical vertebrae showing the beginning of longus colli (Lci) on C7 rib ligament; c) *Moloch horridus*, right ventrolateral view of the cervical and dorsal vertebrae showing two keeled intercentra, the longus colli (Lci) = longus cervicus (Lc), also both muscles (Lci &Lc) originate from rib ligaments only. d) *Calotes versicolor*, one posterior intercentral muscle slip to skull (Ic2-Bop/Oop). e) *Draco fimbriatus*, six posterior intercentral muscle slips to skull (Ic[2-6]-Bop/Oop). Scale bar = 1 mm.



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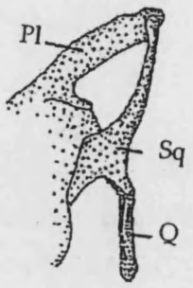

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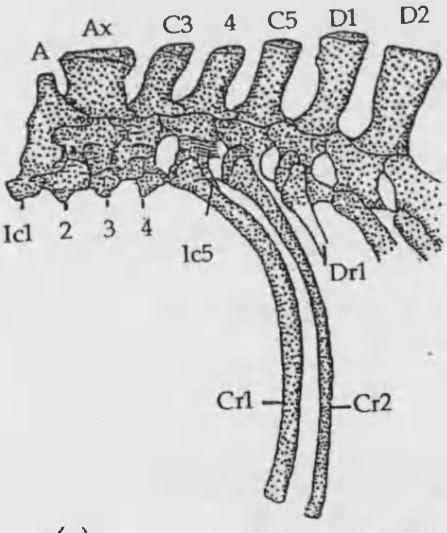

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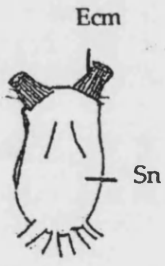
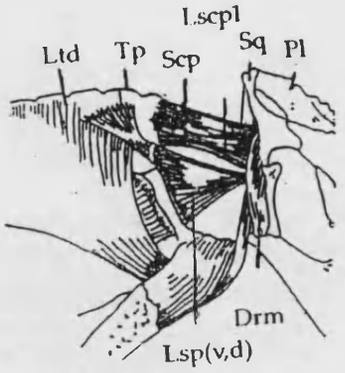


(d)

Plate (4.3.1) *Chamaeleo vulgaris*, a) occipital view of the braincase showing the sharply keeled midline ridge of the supraoccipital where the crista parietalis inferior (Cpi) fused. *C. chamaeleon* b-d, b) left lateral view of the skull showing the parietal (Pl), squamosal (Sq) and quadrate (Q); c) left lateral view of the vertebrae showing 5 cervical vertebrae and 5 keeled intercentra, rib ratio 3+2; d) ventral view of the sternum (Sn) where episternocleidomastoid (Ecm) originates. Scale bar = 1 mm.

(a)



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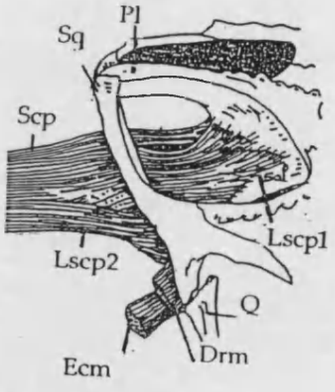


(c)

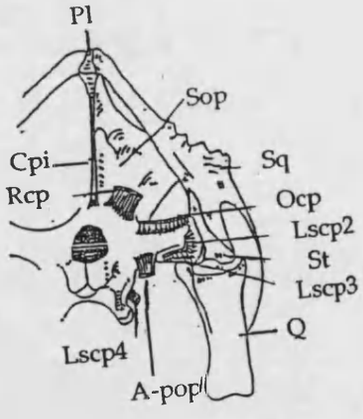


Plate (4.3.2) *Chamaeleo chamaeleon*, (a-b) right lateral view of the skull, a) superficial muscles like depressor mandibulae (Drm), Trapezius (Tp) and latissimus dorsi (Ltd); b) right lateral view of the skull showing the insertion of splenius capitis (Scp) and longissimus capitis 1 (Lscp1) on the supraoccipital; c) occipital view of the skull showing deep muscles which insert mostly on the braincase. Scale bar = 1 mm.

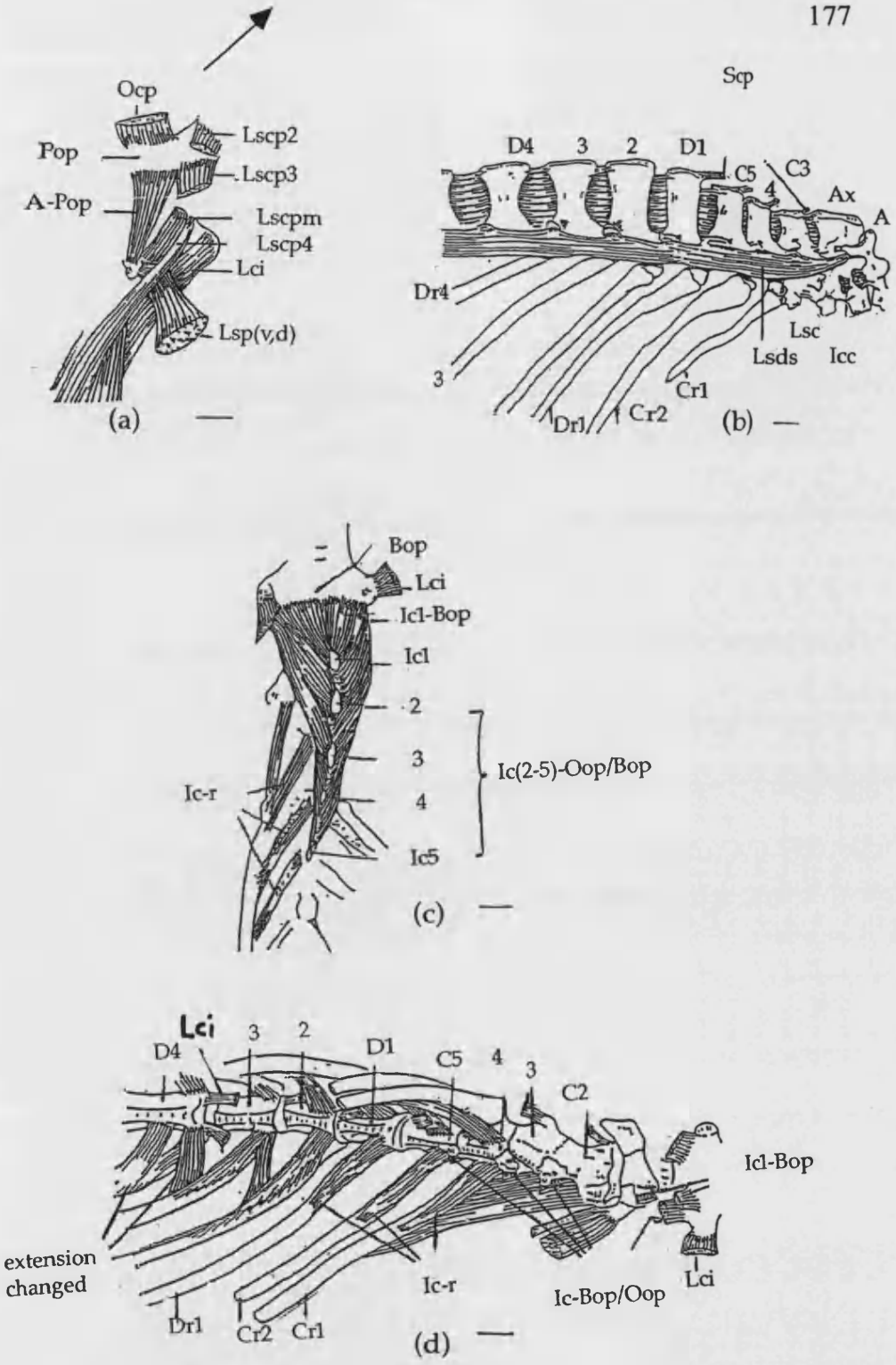
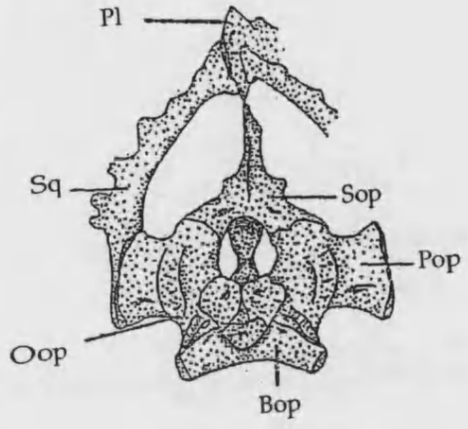
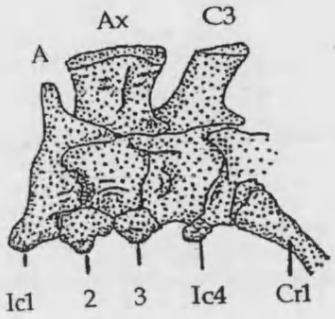


Plate (4.3.3) *Chamaeleo chamaeleon*, a) occipital view of the skull where deep atlas to paroccipital muscle slip (A-Pop) appears beside longissimus capitis 3 (Lscp3); b) right lateral view of cervical and dorsal vertebrae with splenius capitis (Scp) and longissimus dorsi (Lsds) attachment; c) deep ventral view with 5 intercentral muscle slips to skull (Ic[2-5]-Oop/Bop); d) right ventrolateral view of the craniocervical region showing the deep intercentral muscle slips to adjacent rib shafts of cervical and anterior dorsal ribs (Ic-r) where fibre direction is changed, also intercentra are fused to the centrum behind. Scale bar = 1 mm.



(a)



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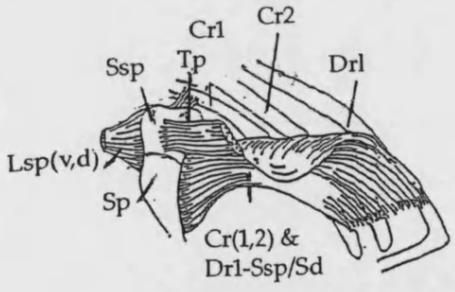

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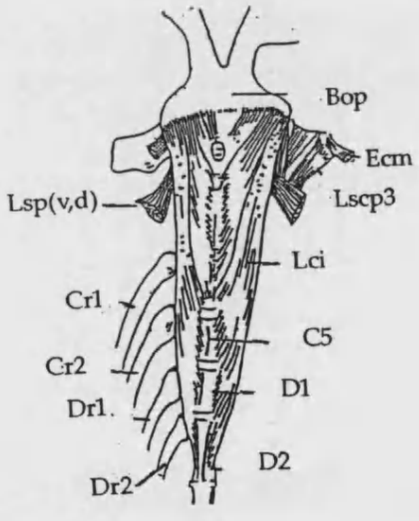


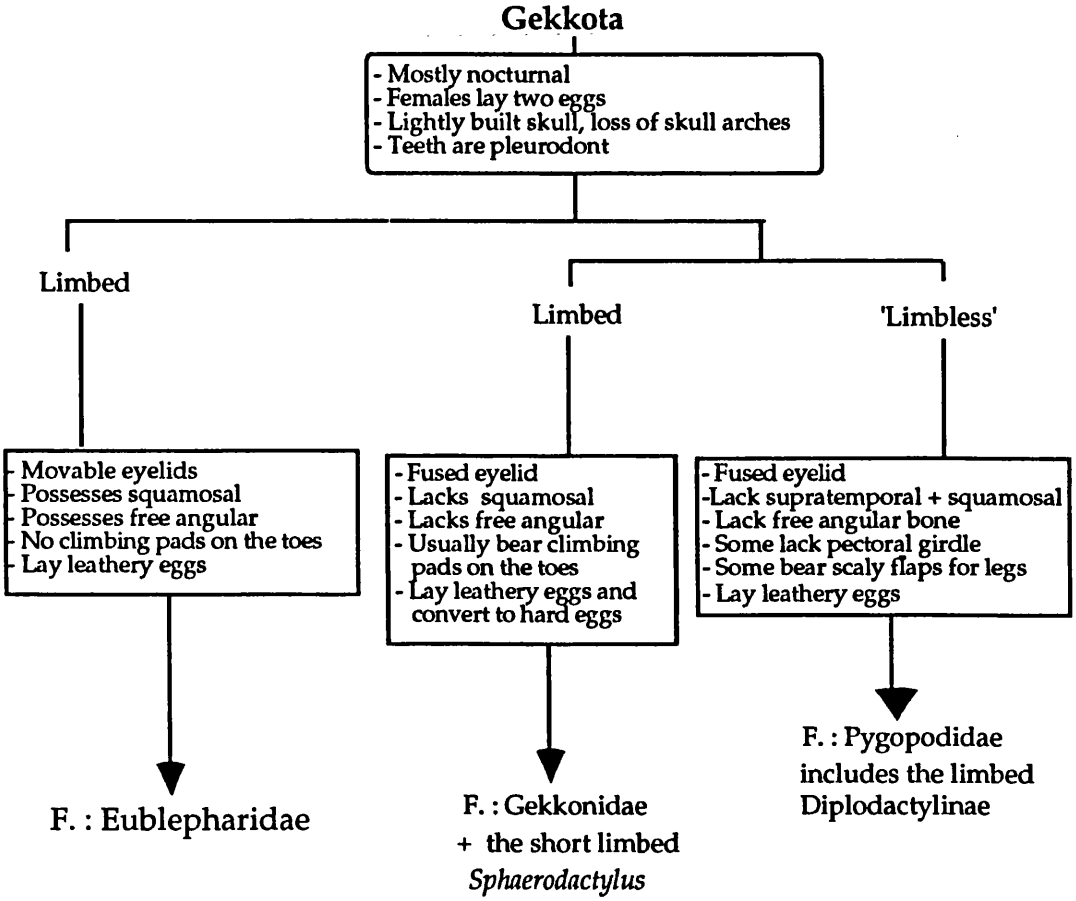
(d)

Plate (4.3.4) a) *C jacksonii*, occipital view of the skull where supratemporal bone (St) is absent; b) C. *chamaeleon*, left lateral view of anterior cervical vertebrae showing intercentra (Ic) are sutured between centra. c) C. *dilepis*, left lateral view of the pectoral girdle and ribs showing the cervical and dorsal ribs to suprascapula/scapulocoracoid muscle slips (Cr[1-2]&Dr1-Ssp/Sd). d) *C. jacksonii*, ventral view of craniocervical region where longus colli (Lci) begins from D2 mid-centrum. Scale bar = 1 mm.

CHAPTER (5)

GEKKOTA

The Gekkota includes three living lineages, the fully limbed geckos (Eublepharidae and Gekkonidae) and the Australasian limbless or flap-footed geckos (Pygopodidae) (Cogger and Zweifel, 1998).



The limbed geckos are a highly diverse group of lizards with 90 genera and more than 900 species. They are terrestrial or arboreal lizards which occupy all continents except Antarctica. The family Eublepharidae consists of 6 genera and about 25 species occuring in Africa, Asia, and North and Central America. Unlike most other geckos, the eublepharids have movable eyelids and their feet lack climbing pads. All species are active at night and have a moderate size of 45-120 mm (adult), e.g. the Leopard gecko *Eublepharis macularis* of south west Asia (Young, 1981; Bauer, 1992). Family Gekkonidae contains 80 genera and about 850

species, and its members are found in all continents around the warmer areas and most oceanic islands (Zug, 1993). Gekkonids differ from eublepharids in several features (see above diagram). They usually bear ridge pads (lamelle) on the toes, covered with tiny bristles (setae) for adhesion to smooth surfaces (Rogner, 1997). They are mostly nocturnal, although some are diurnal, and they have hard -shelled eggs. Examples include: the common house gecko of southern Europe, *Tarentola mauritanica;* the house lizard of Africa, south east Asia, islands of Pacific and South America, genus *Hemidactylus;* the tropical Asian tokay *Gekko gecko ; Phelsuma* and *Uroplatus* of Madagascar and the Indian Ocean Islands; and the tree gecko *Ptychozoon* that has a web of skin along the limbs and body for gliding (Young, 1981; Bauer, 1992; Zug, 1993). The tiny American diurnal short-limbed *Sphaerodactylus* is sometimes included within Gekkonidae, and sometimes in a family of its own. Members of the family Pygopodidae are generally limbless, with a long body and small flattened flaps close to the cloaca which represent the hind limbs. In spite of their size, these flaps can be used for locomotion and defensive behaviour. The group consists of about 36 species that are mostly restricted to Australia with one species found in New Guinea (Bauer, 1992). The limbed Australian and south west Pacific diplodactylines are linked with the Pygopodidae (on biogeography and morphology). Diplodactylines include *Bavayia, Hoplodactylus* and *Oedura* (Bauer, 1992; Zug, 1993), while pygopodidines include the burrower *Aprasia; Delma,* a slender surface lizard; the large diurnal *Lialis burtonis* (59 cm); and the black-headed scaly-foot *Pygopus nigriceps* (Bauer, 1992).

Anatomy of the neck region in Gekkota

Several gekkotans were dissected: *Hemidactylus flaviviridis, Tarentola mauritanica, Phelsuma madagascariensis, Gekko gecko, Chondrodactylus angulifer, Ptychozoon kuhli, Uroplatus fimbriatus* and *Eublepharis macularis.* Skeletons of some gekkonids were also examined: *Chondrodactylus angulifer, Ptychozoon kuhli, Phelsuma guentheri, Gekko smithii, Gehyra marginata* and *Diplodactylus caudicinctus.* I selected genus *Hemidactylus* for the detailed description (*H. flaviviridis* and *H. fasciatus* [skeleton])

Previous work:

Camp, 1923; Broom, 1925; Mahendra, 1950; Underwood, 1954; Romer, 1956; Ganguly and Mitra, 1958; Holder, 1960; Kluge, 1967, 1987; Lécuru, 1968; Hoffstetter and Gasc, 1969; Wahba et al, 1992 c; Zaaf et al., 1999).

Osteology of *Hemidactylus flaviviridis*

(Plate 5.1, 5.2)

Skull

1- Parietal

The mid-posterodorsal margin possesses a posterior process flanked by two wide shallow concavites (plate 5.2c) (where splenius capitis inserts). The posterolateral processes are long and thin and meet the paroccipital processes (where depressor mandibulae internus originates).

2- Squamosal

Absent in gekkonids (Broom, 1925; Romer, 1956; Kluge, 1967). Camp (1923) and Kluge (1967) report that both squamosal and supratemporal are present in some eublepharids.

3- Supratemporal

This is a long narrow bone which extends along the anterior side of the parietal posterolateral processes (where depressor mandibulae internus originates). The supratemporal contacts the parietal and the quadrate (plate 5.1a).

4- Quadrate

This is a wide bone with a flat posterodorsal surface.

5- Retroarticular process

This is well developed.

6- Supraoccipital

Superiorly, the bone is smooth and possesses a dorsolateral rim-like shelf (where rectus capitis inserts) (plate 5.2a).

7- Oto-occipital

The paroccipital processes are narrow with a narrow distal end. The dorsal margin of the process possesses a rim-like shelf (where obliquus capitis inserts). The distal ends of the paroccipital processes bear epiphyses (see the following paragraph). The ventrolateral margins of the oto-occipital are convex and bear a crista tuberalis which is long with both a thick edge close to the basal tubera (convex ventrolateral tip where longissimus capitis 4 inserts), and a thin keeled edge distal to the basal tubera (where the longissimus capitis minor inserts).

8- Paroccipital epiphysis

The paroccipital process possesses a wedge-shaped extension (where episternocleidomastoid inserts) (plate 5.1a).

9- Basioccipital

Each basal tuberculum has one oval epiphyses.

Presacral vertebral column

1- Atlas

The short posterior process bears a dorsal concavity surrounded by a bony fringe, and projects laterally (where deep axis to atlas muscle inserts) (Mahendra [1950] denied the presence of such a process in *H. flaviviridis*, while Ganguly and Mitra [1958] described it as a postzygapophyses for articulation with the axis. My observation support

Ganguly and Mitra's description). The transverse process is short and the first intercentrum is deeply keeled (plate 5.1c).

2- Axis

The postzygapophyses are smooth and straight. Ventrally, the centrum possesses an anterior intercentrum with a lateral crest (where longus cervicus externus inserts). Posteriorly, the centrum meets the third intercentrum (sutured between C2-3), which has two lateral crests (where longus cervicus internus and the rib ligament insert) (plate 5.1e). The position of the intercentra agrees with Holder (1960), whereas Mahendra (1950) described two intercentra on the axis centrum.

3- C3-8

There are 8 cervical vertebrae in total (Hoffstetter and Gasc, 1969) and 8 keeled intercentra (the eighth is very small) (plate 5.1c). The vertebral centra are amphicoelous (Camp, 1923; Kluge, 1967), as in xantusiids (Underwood, 1954; Kluge, 1987). Dorsally, the neural spines increase in height posteriorly and the first tall spines start on C7-8 (where splenius capitis slips originate). The anterior margins of the neural spines are straight (C7-8) or curved (C3-6); the posterior margins are mainly curved. Dorsally, the neural arches are long (C3-4 and C8), or short (C5-7), with smooth, horizontal postzygapophyses. The widths of the third, fourth and eighth centra are equal to the length, while the widths of the fifth, sixth and seventh are greater than the length.

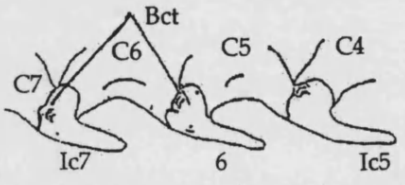


Fig. (5.1) Right ventrolateral view of the cervical vertebrae showing (5-7) intercentra with basal crests (Bct) in *H. flaviviridis*. Scale bar = 1 mm.

Ventrally, a keeled groove runs between the sutured keeled intercentra. The second and third intercentra have posterior lateral crests (where the

superficial and deep longus cervicus muscles insert). All the intercentra possess basal crests where rib ligaments attach. The apex of the second intercentrum is directed posteriorly, while posterior intercentral apices project anteriorly (3-7 intercentra) Fig. (5.1).

4- Anterior trunk vertebrae

The neural spines are long and wide with oval tips. The anterior margins of the spines are curved and smooth. The intercentra are crescentic (Hoffstetter and Gasc, 1969) and are present along the rest of the vertebral column.

5- Ribs

Rib ratio = 3 + 3 + 2. The first cervical rib (C4) is wide and single-headed. The distal ends of the second and third ribs are also wide and bear either expanded cartilaginous ends (*Hemidactylus flaviviridis*), or forked ends (*Hemidactylus fasciatus*) for the rib to suprascapula muscles. Mahendra (1935) incorrectly interpreted the bifurcation as the presence of an "uncinate" process. The fourth and fifth ribs are rounded and long with narrow cartilaginous ends. The dorsal ribs are long and attach to the sternum. The cervical rib ligaments connect the ribs with the intercentra (keeled), while the trunk rib ligaments join the intercentra (flat) with the transverse processes.

Pectoral girdle

1- Sternum

This is well-developed flat bone.

2- Interclavicle

In *Hemidactylus flaviviridis*, the cruciform interclavicle possesses long wide lateral arms with pointed ends (where episternocleidomastoid originates), and a wide posterior stem that tapers posteriorly (ends on the sternum) (Kluge, 1967, 1987) (plate 5.1b).

3- Clavicle

A well developed curved bone.

4- Suprascapula/capulocoracoid

A wide well-developed scapulocoracoid with a large cartilaginous suprascapula (see chapter 1).

Muscles of *Hemidactylus flaviviridis*

(Plate 5.2 - 5.3)

Superficial muscles

1-Depressor mandibulae (internus and externus)

The muscle originates from the parietal and supratemporal (internus), and from the muscle fascia of splenius capitis (externus) (plate 5.2b). Both branches insert (overlapping each other) on the retroarticular process (long concavity).

2- Cervicomandibularis

Originates from the muscle fascia of the splenius capitis, and inserts on the ventral side of the articular.

3- Constrictor colli

See chapter 2.

4- Trapezius

Originates from the mid-dorsal line (plate 5.2a) (Zaaf et al., 1999), and inserts on the anterior margin of the suprascapula and clavicle.

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

1-Episternocleidomastoid

Originates from the interclavicle (plate 5.1b), and inserts on the external epiphysis of the paroccipital process. However, Wahba et al. (1992c) reported that the muscle inserts on the posterolateral part of the quadrate in *Tarentola*. This could be related to the size and way of attachment of a muscle.

2- Clavicle dorsalis

Originates from the posterolateral side of the supratemporal and muscle fascia, and inserts on the anteroventral margin of the clavicle.

3-Levator scapula dorsalis and ventralis

Both originate from the atlas transverse process, and insert on the anterior border of the suprascapula.

4- Ribs to suprascapula/scapulocoracoid muscle slips

Originates from the distal end of the first, second and third ribs, and inserts on the inner dorsal margin of the suprascapula. The fourth and fifth rib muscle slips are connected to the posterior margin of the suprascapula.

Deep muscles

1- Obliquus capitis externus and internus

Both layers originate from the anterior cervical spines (C4-2), and insert on the dorsal margin of the paroccipital process close to the suture with the supraoccipital.

2- Rectus capitis

Originates from C1 neural spine. Wahba et al. (1992c) reported the origin as from C1 and C2 in *Tarentola*. It inserts on the dorsal margin of the supraoccipital. This could be related to the muscle size.

3- Splenius capitis

Originates posteriorly above the cervical spines, and extends anteriorly as single trunk to insert on the parietal posterodorsal median process.

4- Spinalis and semispinalis muscles

a) Spinalis capitis

Originates posteriorly from the cervical spines, and inserts on the parietal posterodorsal median process (internal to splenius capitis).

b) Spinalis/semispinalis cervicus

Not investigated during dissection.

c) Spinalis/semispinalis complex

See chapter 1.

5- Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches along C5 and extends anteriorly to insert on the dorsolateral side of the parietal towards the postorbital bone (plate 5.2c). The muscle extends and inserts (in a triangle) anterior to the splenius capitis insertion (Wahba et al. 1992c - *Tarentola annularis*) (plate 5.2a).

c) Longissimus capitis 2

Branches along C5, and runs anteriorly to insert on the lateral and ventral sides of the paroccipital processes (L-shaped) (Wahba et al., 1992c).

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches ventrally along C4, and inserts anteriorly on the ventrolateral tip of the oto-occipital (near the basal tubera) (plate 5.3a).

f) Longissimus capitis minor

Branches from the atlas posterior process (see chapter 1) and inserts on the ventrolateral margin (crista tuberalis = sharp rim) of the oto-occipital (plate 5.3a).

6- Iliocostalis muscles

a, b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates centrally from the 9th flat intercentrum (between C8 and D1) as a tendinous bundle (plate 5.3b). The muscle starts narrow (as muscle

fibres) on the C8 centrum, and continues along C6-7 centra and the rib ligaments. Then it becomes wider as it is joined by slips of muscle originating from the anterior intercentral apices and rib ligaments. Finally the muscle inserts (as muscle fibres) on the basal tubera.

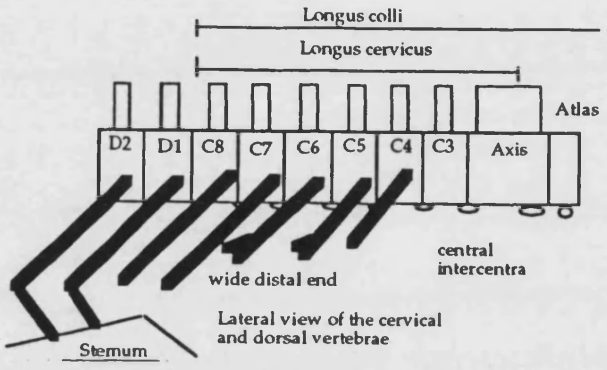


Diagram (5.1) Right lateral view of the cervical verterbrae showing the start of longus colli and cervicus in *H. flaviviridis*

b) Longus cervicus (superficial + deep)

The superficial longus cervicus branch originates from the eighth intercentrum and extends anteriorly as it is joined by a series of muscle segments which originate from the anterior margins of the intercentra before ending on the posterior lateral crests of the second intercentrum (plate 5.3b). The deep longus cervicus branch originates from the flat ninth intercentrum (deep to the longus colli), and is joined anteriorly by slips starting from the intercentra and rib ligaments before inserting on the posterior lateral crests (> shaped) of the third intercentrum. The branches insert deep to one other into the posterior margin of the second and third intercentra (lateral crests). The longus colli is equal in length to longus cervicus.

8- First intercentral muscle slip to basioccipital

It originates ventrally from the first intercentrum and inserts on the basioccipital, partially deep to the longus colli.

9- Posterior intercentral muscle slips to oto-occipital

Ventrally, the muscles originate from the second and third intercentra, and insert on the concavity at the ventral end of the oto-occipital deep to the first intercentral muscle to basioccipital (plate 5.3b).

Very deep muscles

1- Deep second intercentral muscle to C4 rib ligament

The muscle appears after removing the longus cervicus muscle slips, and runs deep from the posterior apex of the second intercentrum to insert on the rib ligament/transverse process of C4 ventrally (~ iliocostalis muscle).

2- Cervical and trunk central tendon

The last posterior keeled intercentrum (~ eighth keeled intercentrum) has a tendon which extends posteriorly along the flat intercentra and centra of the dorsal vertebrae.

Comparison of the osteological and muscular features within Gekkota

In their craniocervial morphology, the neck anatomy in the gekkotans examined (*Tarentola mauritanica, Phelsuma madagascariensis, Gekko gecko, Chondrodactylus angulifer, Ptychozoon kuhli, Uroplatus fimbriatus, Eublepharis macularis* [dissected]; and *Hemidactylus fasciatus, Ptychozoon kuhli, Phelsuma guentheri, Gekko smithii, Gehyra marginata* and *Diplodactylus caudicinctus* [skeleton]) seems to be remarkably consistent. They all share a set of osteological and muscular features as follows:

1) Similarities between gekkotans including eublepharids:

Excluding general similarities found in other lizards.

- The paroccipital processes have lateral epiphyses.
- The second and third sutured intercentra have lateral and basal crests.

- The second and third cervical ribs possess wide distal ends which are sometimes forked.
- Trapezius inserts on the suprascapula + clavicle.
- Episternocleidomastoid inserts on the paroccipital epiphysis.
- Deep rib to suprascapula muscle slips are absent.
- Spinalis capitis is present.
- Splenius capitis extends above cervical spines.
- Longissimus capitis 1 inserts in a triangle shape on the posterolateral side of the parietal.
- Longissimus capitis minor inserts dorsally on the oto-occipital near the crista tuberalis and close to the base of the paroccipital process.
- Longus colli and cervicus usually originate together centrally (centra or intercentra), and extend anteriorly adding slips from the keeled intercentra and rib ligaments. Both muscles are equal in length. The longus cervicus is well-developed and inserts anteriorly in two layers (deep on the third intercentrum, and superficial on second intercentrum).
- The first intercentral muscle slip inserts ventrally on the basioccipital partially deep to longus colli.
- Posterior intercentral muscle slips insert on the oto - occipital deep to the first intercentral muscle slip insertion.
- A cervical and trunk central tendon is present.

<u>2) Variation between gekkotans including eublepharids:</u>

Despite the many similarites between the different geckos examined, they show some variation at intraspecific (e.g., *Gekko gekko* [small + large]) and interspecific levels (e.g., *Gekko gecko* and *Gecko smithii*. See discussion section on intra-and interspecific variation), as well as between genera and families

(Plate 5.4 - 5.5 - 5.6)

<u>Variation between genera and families</u>

- The squamosal is absent in all gekkonids, but present in eublepharids where it meets the quadrate and is shorter than the supratemporal (plate 5.4c). Kluge (1967) recorded the squamosal to be larger than the supratemporal, except *E. hardwickii* where the squamosal is large and the supratemporal is absent.

- The axis anterior intercentrum usually has single lateral crests, but in *Gekko* spp., there are double lateral crests.

- The number of keeled intercentra is usually 8, but in *U. fimbriatus* and *E. macularis*, there are 5-7 (plate 5.4d).

- The rib ratio = 3 + 3 + 2 except in *U. fimbriatus* where it is 2 + 4 + 2. The number of the cervical ribs is 5 except in *U. fimbriatus* where it is 6.

- The interclavicle varies in shape, such that the lateral arms range from long and narrow in *T. mauritanica*, to short and wide in *D. caudicinctus*, *Gekko* spp. and *E. macularis*. The posterior process is short and narrow in *U. fimbriatus* or long and wide in *E. macularis*. In some gekkonids, the lateral processes are absent (Lécuru, 1968)

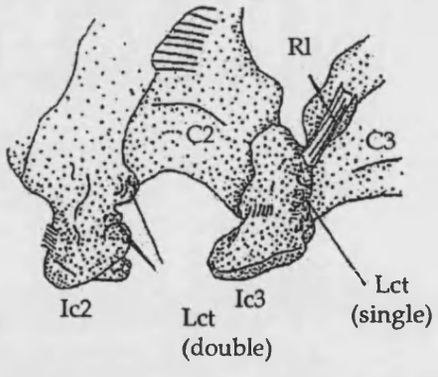


Fig. (5.2) Left ventrolateral view of the cervical vertebrae showing double lateral crests (Lct) on the second intercentrum, and one lateral crest on the third intercentrum in *G. gecko*. Scale bar = 1 mm.

- The clavicle has a ventral fenestra (most examined taxa), or is solid (*U. fimbriatus*) (plate 5.4f).

- Depressor mandibulae internus originates from the supratemporal (most gekkonids), or the parietal +/- supratemporal (*G. gecko*,

H. flaviviridis and *Phelsuma*), or from the quadrate only (*U. fimbriatus*). In *E. macularis* it originates from the parietal+ lateral skull components + quadrate + paroccipital epiphysis (plate 5.6a). The externus branch usually originates from muscle fascia except in *G. gecko* and *C. angulifer* where it arises from muscle fascia + parietal, and in *U. fimbriatus* from muscle fascia + supratemporal + quadrate (plate 5.5c).

- Episternocleidomastoid originates from the interclavicle except in *E. macularis* where it begins from the clavicle and interclavicle.
- Clavicle dorsalis inserts on the muscle fascia of longissimus capitis 1 except in *H. flaviviridis* (muscle fascia and supratemporal).
- Ribs to suprascapula/scapulocoracoid muscle slips extend from the cervical ribs to the suprascapula, except in *U. fimbriatus* where they arise from cervical + dorsal ribs.
- The obliquus capitis muscle extends anteriorly as one layer to insert on the skull except in *H. flaviviridis, C. angulifer* and *U. fimbriatus* (as two layers: externus + internus) (plate 5.5c). The muscle inserts on the paroccipital process only, except *U. fimbriatus* (paroccipital process and quadrate).
- Spinalis capitis usually originates from the posterior cervical vertebrae, but in *U. fimbriatus* it branches anteriorly to attach on the axis neural spine before its final insertion on the parietal.
- Splenius capitis usually originates from the muscle fascia above the neural spine, but in *E. macularis* it originates centrally from the neural spines and laterally from the muscle fascia.

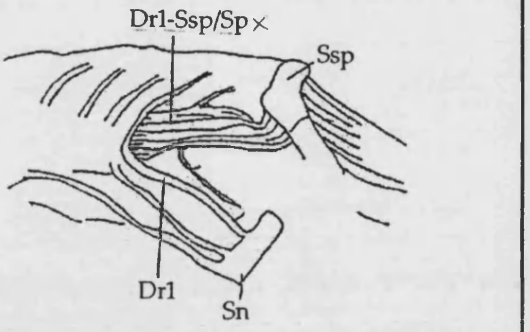


Fig. (5.3) Right ventrolateral view of the pectoral girdle and sternal ribs showing dorsal rib to suprascapula/scapulocoracoid muscle slips (Dr1-Ssp/Sd) in *U. fimbriatus*. Scale bar = 1mm

- Longissimus capitis 1 usually inserts on the parietal (triangular area) anterior to the splenius capitis insertion, but in *U. fimbriatus* and *C. angulifer*, the muscle inserts on the mid-posterior edge of the parietal beside the splenius capitis insertion. In *U. fimbriatus*, the muscle has an extra insertion on the supratemporal (plate 5.5c).
- Longissimus capitis 2 usually inserts on the ventral side of the paroccipital process, but in *E. macularis* the muscle inserts on the lateral end of the paroccipital process (plate 5.6a).
- Longissimus capitis 4 branches ventrally, to insert on the convex ventrolateral tip of the oto- occipital except in *E. macularis* (laterally on oto-occipital and basioccipital) (plate 5.6a).
- Iliocostalis major extends lateral to longus colli, except in *U. fimbriatus*, where the muscle also branches ventrally to insert on the longus colli close to the C4 rib head by a tendon sheet (Lci-Icm), but it does not attach to the intercentra (plate 5.5b).
- Longus colli usually originates from the ninth intercentrum, except in *G. gecko* (ninth intercentrum and C8 rib), *E. macularis* (C7 posterior centrum) (plate 5.6b) and *U. fimbriatus* (tenth intercentrum).
- Longus cervicus originates from ninth intercentrum, except *P. madagascariensis*, *G. gecko* and *P. kuhli* (eighth intercentrum), and in *E. macularis* (C7 centrum) (plate 5.6c).

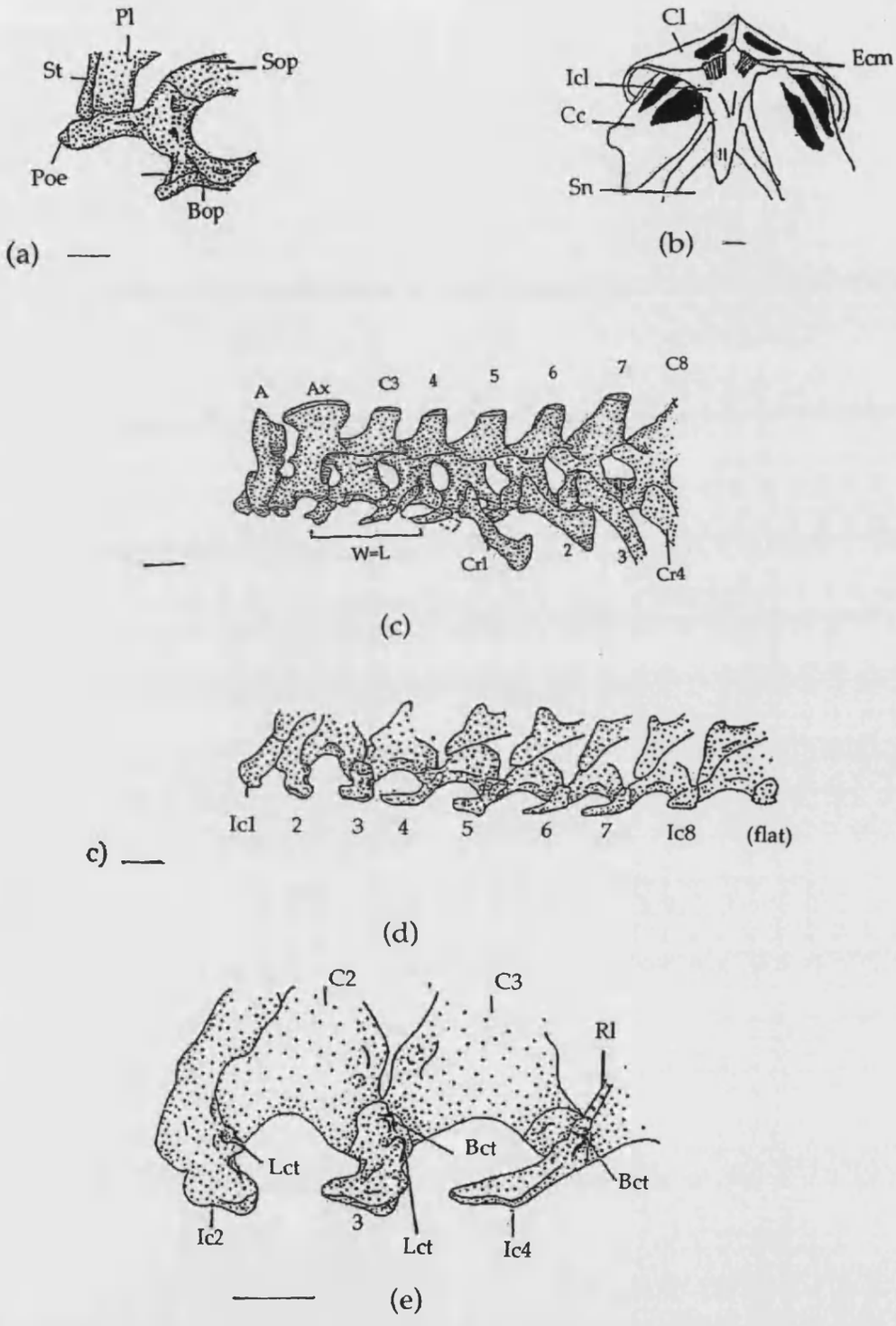
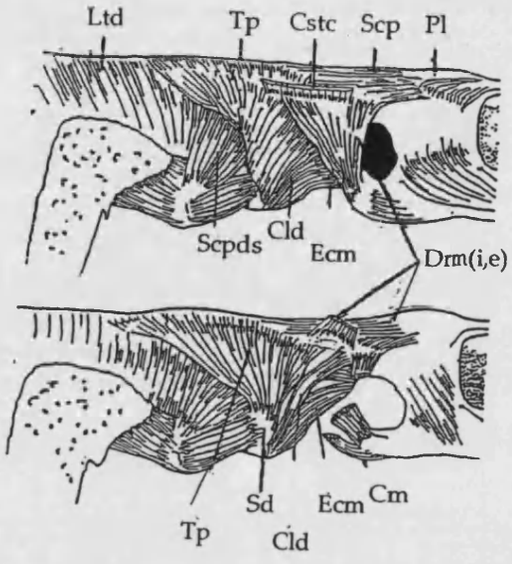


Plate (5.1) a) left posterolateral aspect of skull in *Chondrodactylus angulifer* – paroccipital epiphyses (Poe) and cristae parietalis (Cts) are present; b) ventral view of pectoral girdle in *Hemidactylus fasciatus* – cruciform interclavicle (Icl) and clavicle (Cl) with fenestra. Left lateral view of the cervical vertebrae in *Gekko smithii*, c) the width (W) of anterior cervical centra are equal to the length (L). Left ventrolateral view of the cervical vertebrae in *H. fasciatus*, d) 8 keeled intercentra (Ic), e) intercentra mostly have lateral and basal crests (Lct & Bct). Scale bar = 1 mm.

a)



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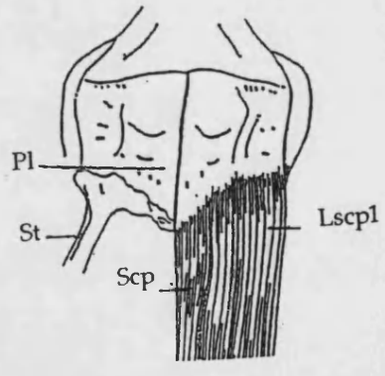
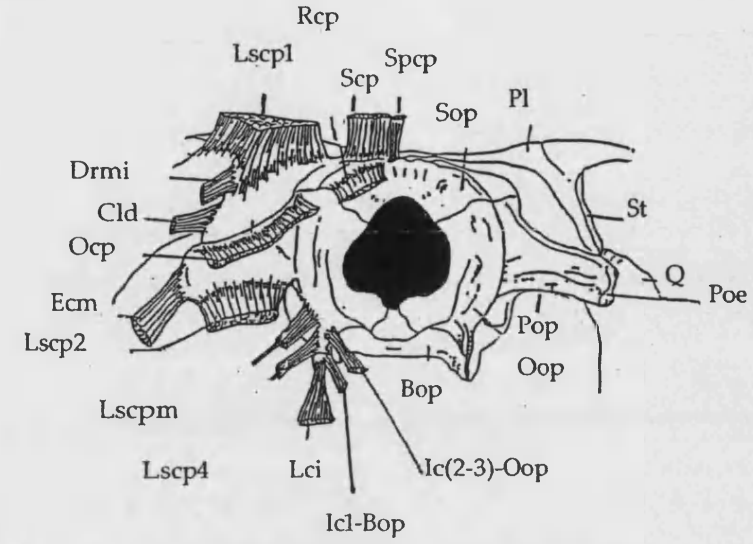
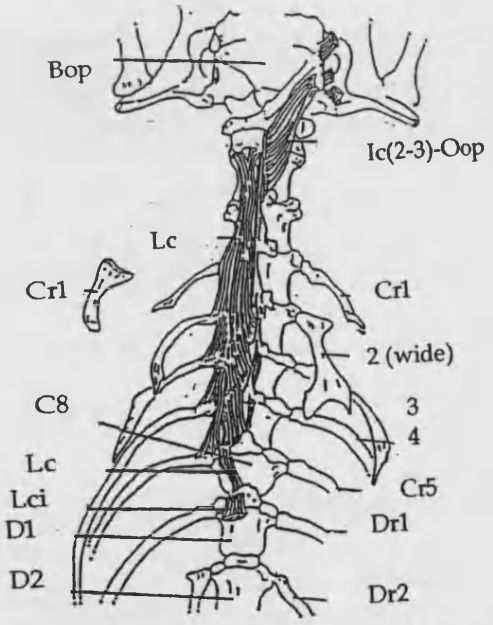


(c)

Plate (5.2) *Hemidactylus flaviviridis*, right lateral view of the craniocervical region, a) superficial muscles depressor mandibulae (Drm), trapezius (Tp), latissimus dorsi (Ltd), also scapula dorsalis (Scpds); b) cervicomandibularis (Cm) and intermediate muscles episternocleidomastoid (Ecm), clavicle dorsalis (Cld); c) insertion of splenius capitis (Scp) and longissimus capitis 1 (Lscp1) on parietal. Scale bar = 1 mm.



(a)



(b)

Plate (5.3) *H. flaviviridis*, a) occipital view of the skull, showing superficial, intermediate and deep muscles, depressor mandibulae (Drm), episternocleidomastoid (Ecm), clavicle dorsalis (Cld), obliquus & rectus capitis (Ocp & Rcp), spinalis capitis (Spcp), splenius capitis (Scp), longissimus capitis 1,2,4 and minor (Lscp1,2,4 & m) origin and insertion; b) longus cervicus (Lc) and intercentral muscle slips to skull (Ic[2-3]-Oop) Scale bar = 1 mm.

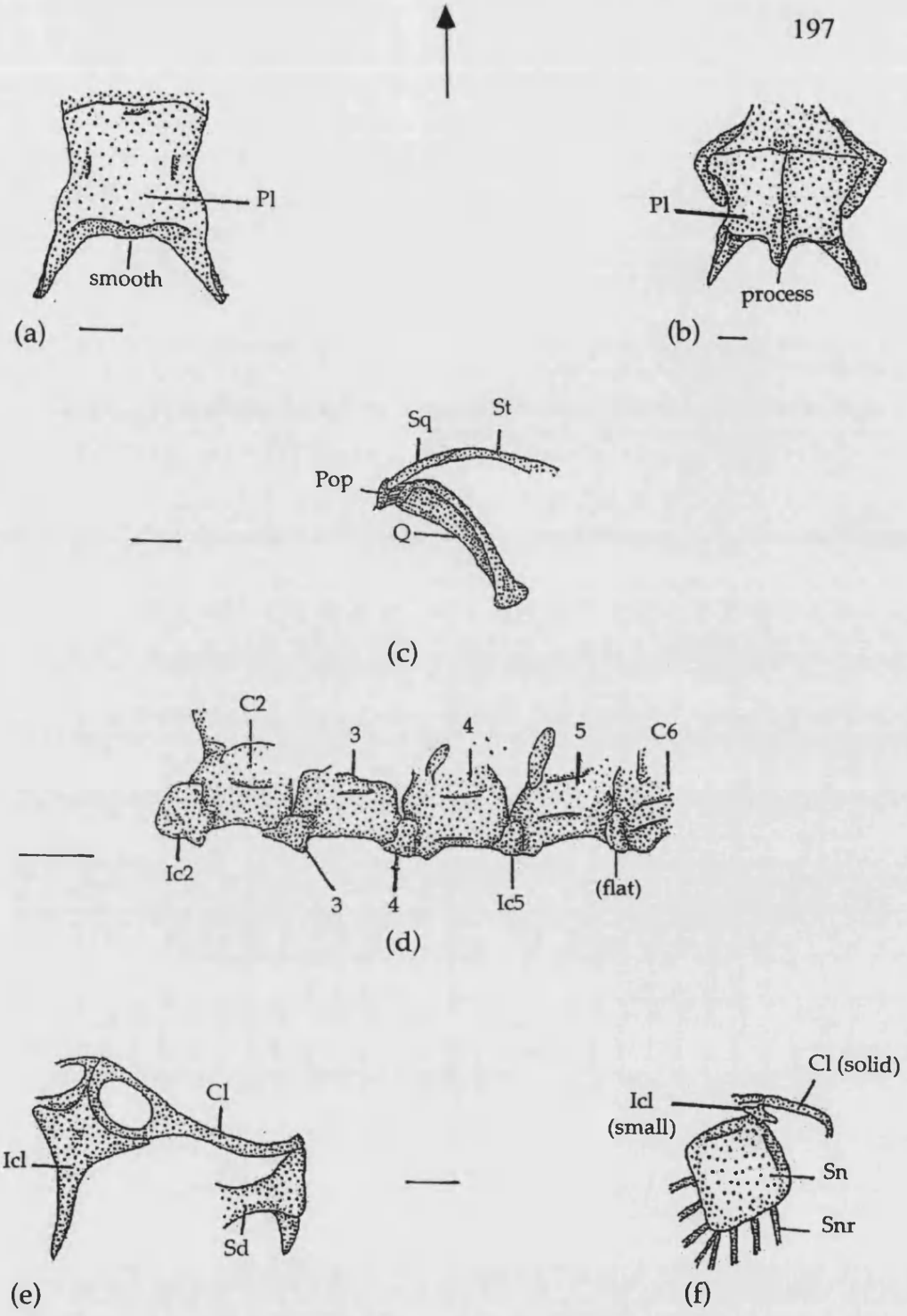


Plate (5.4) a-b) dorsal view of the skull in gekkotans with various parietal (Pl) posterodorsal margins and processes in *Eublepharis macularis*(a), and *Gekko smithii* (b); c) right lateral view of the skull in *E. macularis*, with squamosal (Sq) and supratemporal (St); d) left lateral view of cervical vertebrae with 4 keeled intercentra in *E. macularis*. e-f) Ventral view of pectoral girdle in gekkotans with various clavicle (Cl) (solid or perforate) and interclavicle shapes (Icl), e) *C. angulifer*; f) *U. fimbriatus* (solid clavicle). Scale bar = 1 mm.

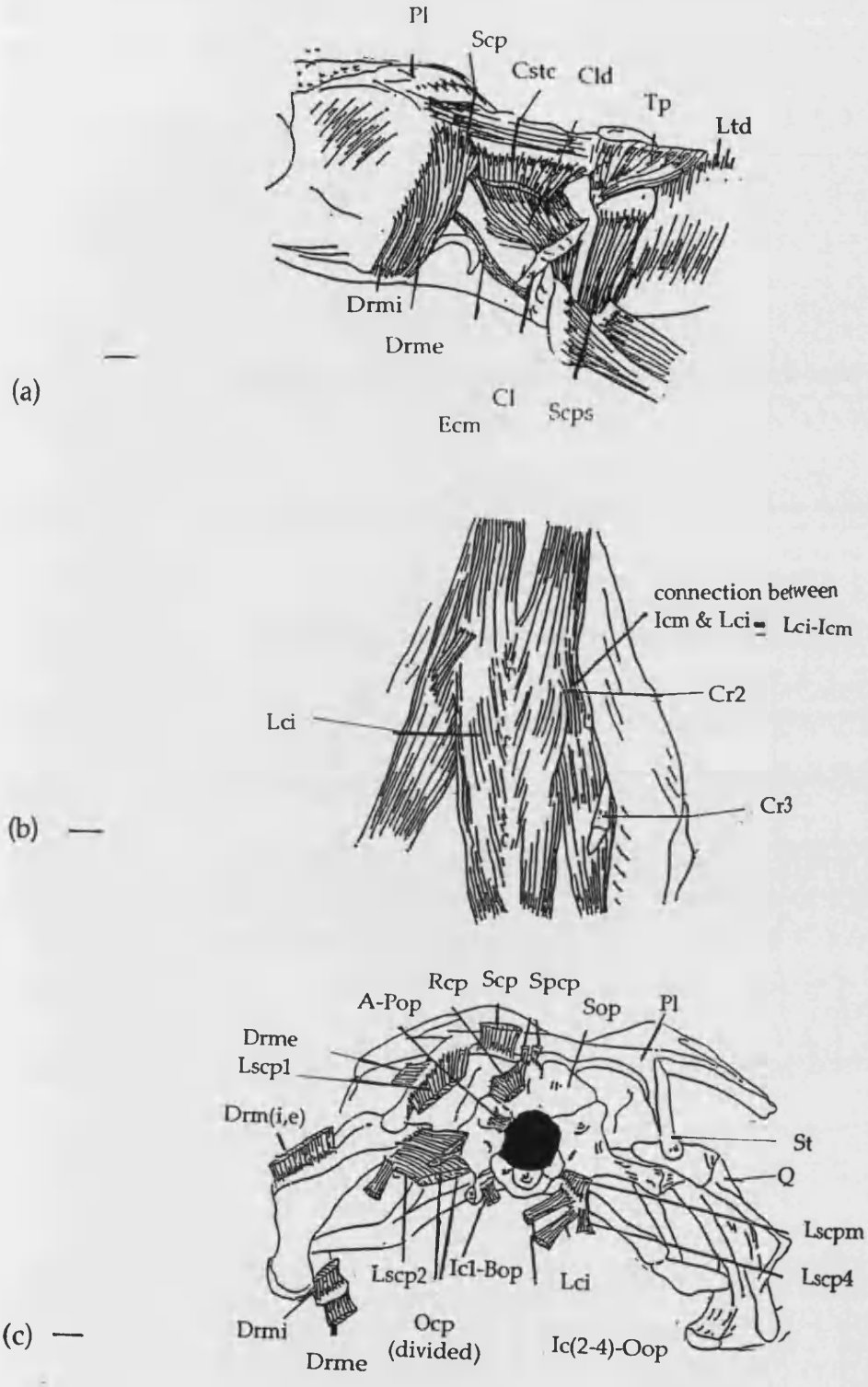
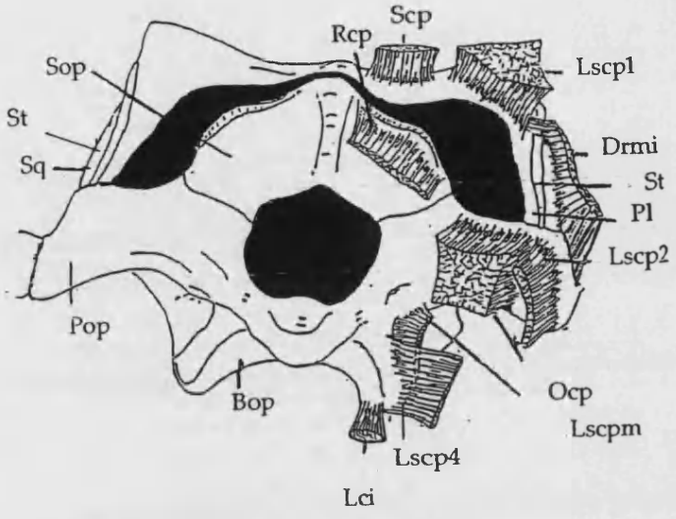
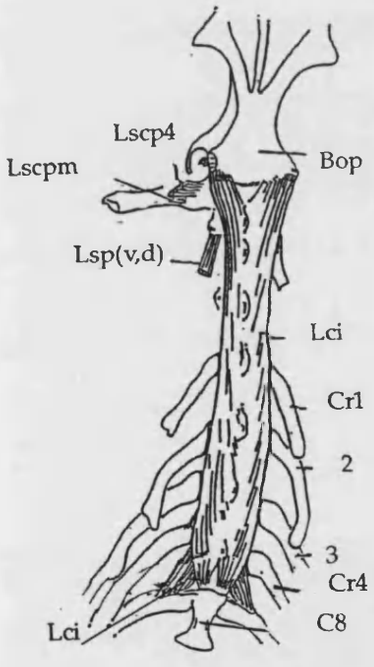


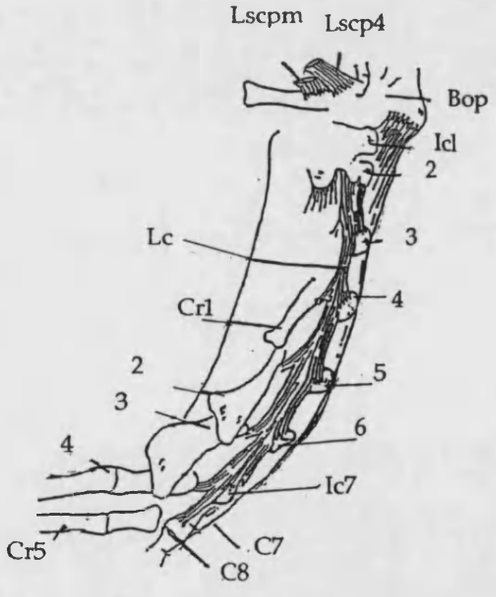
Plate (5.5) *U. fimbriatus*, a) left lateral view of the craniocervical region with most superficial and intermediate muscles, depressor mandibulae (Drm), trapezius (Tp), episternocleidomastoid (Ecm), clavicle dorsalis (Cld); b) ventral view of the cervical region where longus colli (Lci) is connected to iliocostalis major (Icm) =Lci-Icm; c) posterior view of the skull with obliquus capitis (Ocp) inserting on the quadrate (Q) and paroccipital process (Pop). Scale bar = 1 mm.



(a)



(b)



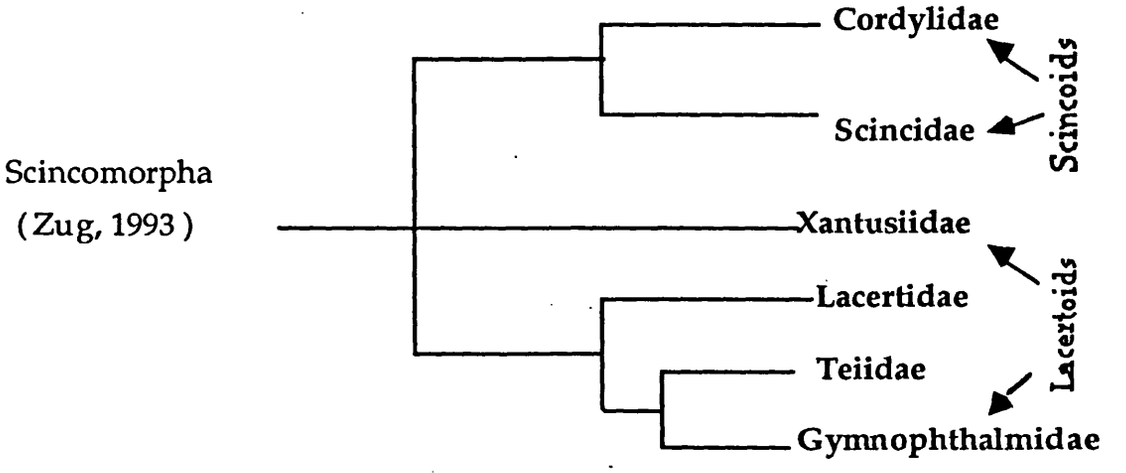
(c)

Plate (5.6) *E. macularis*, a) posterior view of the skull with most superficial and deep muscle insertions, depressor mandibulae (Drm), splenius capitis (Scp), longissimus capitis 1,2,4 & minor (Lscp1,2,4 & m), longus colli (Lci); b) ventral view of the cervical vertebrae showing the longus colli (Lci) origin and insertion; c) right ventrolateral view of the longus cervicus (Lc) origin and insertion. Scale bar = 1 mm.

CHAPTER (6)

SCINCOMORPHA

Scincomorpha is one of the representative subgroups of Autarchoglossa. The families included are Scincidae, Cordylidae, Teiidae, Lacertidae, Xantusiidae and Gymnophthalmidae.



Family: Scincidae

This is the largest lizard family, with around 1,300 species in about 100 genera. Scincids are cosmopolitan in their distribution (tropical and temperate regions), although they are less dominant in Europe, north Asia, South America, and much of North America. Those scincids which mostly live mainly on the surface are usually limbed; reduced limbed or limbless forms are generally burrowers. Nearly all members of the Scincidae have cylindrical bodies that are continuous with the head without external evidence of the neck. Their length ranges from 2.8 mm to 350 mm, and their colour is mostly grey or brown although some species are green or blue. The overlapping scales are smooth and regular. Four subfamilies have been recognized within Scincidae (Zug, 1993): feylinines, a group of small tropical limbless burrowers from central and west Africa; acontines,

limbless sand or soil-dwellers of southern Africa; scincines, a group with a world wide distribution, e.g. *Scincus scincus* of the Sahara, which show a tendency towards degeneration of the limbs and elongation of the body (sand 'swimmer' using shoveling movements of limbs and a serpentine motion, Mertens, 1960); and lygosomines, the largest rock-dwelling group of Australia, islands of the Pacific, Asia, Africa and Central and South America, e.g. *Egernia* and the prehensile tailed skinks of the Soloman Islands, the large *Corucia zebrata* (Young, 1981; Halliday and Adler, 1986; Bauer, 1992; Zug, 1993).

Family: Cordylidae (girdle-tailed lizards)

The cordylids include about 10 genera and 50 species and occur in Africa, south of the Sahara, and Madagascar. During the Eocene (57 - 37 million years ago), cordylids occured in Europe. All species are diurnal and many possess heavy bony keeled osteoderms on the body. Their length ranges between 50 - 275 mm., and they are mainly rock-dwellers, although some live in grassland. Most species are fully limbed with flattened bodies and heads, but some have reduced limbs. The family includes *Cordylus, Gerrhosaurus, Chamaesaura* and *Zonurus* (Webb et al., 1978; Halliday and Adler, 1986; Bauer, 1992; Zug, 1993).

Family: Teiidae

The family includes about 40 genera with approximately 200 species which occur in the New World (South and Central America and warmer parts of North America). Teiids may be closely related to the Old World European lacertids and inhabit a wide range of environments from the rain forest to desert areas. They include carnivores and herbivores, and have elongated bodies with pointed heads that bear large scales. Their necks and trunks possess small granular plates, and the tails are long. The limbs range from

well developed to reduced. Body length ranges from 70 - 500 mm., but mostly < 130 mm. One example is the Jungle-runner, *Ameiva ameiva*, which has a well-developed limbs and occupies a wide range of habitats in southern Mexico to tropical South America (Webb et al., 1978; Bauer, 1992; Zug, 1993).

Family: Gymnophthalmidae

This diverse family includes around 30 genera and 140 species which inhabit Central and South America. They are small, sometimes reduced-limbed lizards which are mostly active at night. In burrowing forms, the hind limbs are reduced more than the forelimbs, e.g. *Bachia* (Bauer, 1992; Zug 1993).

Family: Lacertidae (Wall and Sand lizards)

The lacertids inhabit Europe, Africa, Asia and the Indo-Australian region, and include about 200 species. The size ranges from 40 - 220 mm. The body is elongated with a conical head and a distinct neck; the tail is long and the limbs are well developed. Members of this family feed mostly on small invertebrates, other lizards, snakes and young mammals. The lacertids are similar to the teiids in lifestyle and live on open ground and sandy places. One example is the fringe-toed lacertid, *Acanthodactylus*, from North Africa and the Middle East. These are specialized for sand dwelling and occupy different habitats in the Sahara. Another example is *Lacerta*, a genus of mainly insectivorous lizards that is common in Europe (Webb et al., 1978, Bauer, 1992; Zug, 1993).

Family: Xantusiidae (night lizards)

These limbed gecko-like forms are distributed in Cuba, Panama to Central Mexico, and the South Western United States. They include 4 genera and

around 19 species. They are usually considered related to lacertids, teiids and gymnophthalmids (Halliday and Adler, 1986; Bauer, 1992; Zug, 1993).

Anatomy of the neck region in Scincidae

The scincid taxa dissected were *Scincus mitranus, Scincus alifasciatus laterimaculatus, Tiliqua nigrolutea* and *Tiliqua rugosas. Scincus mitranus* was dissected in more detail. A skeleton of *Scincus fasciatus* was also examined.

Previous works:

El-Toubi, 1938; Hoffstetter and Gasc, 1969; Greer, 1970; Estes et al., 1988.

Osteology of *Scincus mitranus*

(Plate 6.1.1)

Skull

1- Parietal

The mid-posterodorsal margin of the parietal possesses a small posterior process with shallow bilateral concavities (where splenius capitis inserts). The posterolateral processes, which are long and wide, extend towards the paroccipital process (where depressor mandibulae internus and externus originate and episternocleidomastoid, obliquus capitis externus; longissimus capitis 1 and 2 insert).

2- Squamosal

This splint-like bone is longer than the supratemporal (plate 6.1.1b) (depressor mandibulae internus originates and episternocleidomastoid inserts) and does not meet the paroccipital process.

3- Supratemporal

This wide elongated bone extends along the lateral side of the posterolateral process of the parietal and the lateral margin of the paroccipital process

(where episternocleidomastoid muscle, obliquus capitis externus and longissimus capitis 2 insert). It also contacts the squamosal and quadrate.

4- Quadrate

This is wide bone has a posterodorsal process that is slightly exposed (where episternocleidomastoid muscle inserts).

5- Retroarticular process

A well-developed wide posterior process (where depressor mandibulae inserts).

6- Supraoccipital

It has a rounded midline ridge (plate 6.1.1b) (where rectus capitis internus and externus insert).

7- Oto-occipital

The paroccipital process is wide (where obliquus capitis internus and externus insert laterally). The ventral end of the oto-occipital near the basioccipital has a curved ridge (where intercentral muscle slips insert).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera have elongated narrow epiphyses (where longus colli, longissimus capitis 4 and part of longissimus capitis minor insert). The area between the basal tubera bears a shallow linear ridge (where the superficial first intercentrum muscle inserts).

Presacral vertebral column

1- Atlas

This possesses short posterior processes and wide transverse processes. The first intercentrum is deeply keeled.

2- Axis

The posterodorsal process of the neural spine is high and oval (plate 6.1.1f). The postzygapophyses have shallow tubercles. Each transverse process is wide and projects strongly. Ventrally, the keeled centrum has an anterior second intercentrum with lateral crests, and a posterior fused third intercentrum.

3- C3-8

There are 8 cervical vertebrae, and 7 keeled intercentra (plate 6.1.1f). Their height starts to increase on C8. The anterior and posterior margins of the neural spines are smooth and curved. The spines are inclined (<60°) relative to the centra. The postzygapophyses are smooth and horizontal. Laterally, the width and the length of the centra are nearly equal with no zygosphenes and zygantra. However, Estes et al. (1988) recorded the presence of such accessory articulations in some scincids. Ventrally, the centra are keeled between the adjacent intercentra, each of which is fused to the centrum in front (Estes et al., 1988). Most intercentra have basal crests (where rib ligaments attach) (plate 6.1.1e).

4- Anterior dorsal vertebrae

The neural spines are long, wide and have compressed dorsal tips (where spinalis/semispinalis muscle complex and longissimus dorsi attach). The anterior margins are smooth and curved with a wide crest.

5- Ribs

Rib ratio = 3 + 3 + 2 (El-Toubi, 1938). The distal ends of the anterior cervical ribs (C4-6) are forked with cartilaginous ends (posterior process [iliocostalis muscle slips], ventral process [suprascapula muscle slips]). Ventrally, they have ligaments that connect the ribs to the basal crests of the intercentra.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

It articulates with the suprascapula dorsolaterally (plate 6.1.1c) (where trapezius inserts).

3- Interclavicle

This cruciform bone has long narrow lateral, anterior and posterior processes (plate 6.1.1d) (where episternocleidomastoid originates) (Greer, 1970).

4, 5- Scapulocoracoid and suprascapula

The scapula is wide and bears a curved wide suprascapula.

Muscles of *Scincus mitranus*

(Plate 6.1.2 – 6.1.3)

Superficial muscles

1- Depressor mandibulae (internus and externus)

The depressor mandibulae internus originates from the parietal and squamosal, while the externus starts from the parietal (tendon) and muscle fascia of longissimus capitis (plate 6.1.2d). Both muscles insert on the retroarticular process (by overlapping each other).

2- Cervicomandibularis

Originates from the muscle fascia of longissimus capitis 2 dorsally, and inserts on the articular.

3- Constrictor colli

A wide flat semi-rounded muscle that runs along the long neck region (plate 6.1.2a) (see chapter 1).

4- Trapezius

Originates from the mid-dorsal line, and inserts on the clavicle and suprascapula.

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arms of the interclavicle (muscle fibres), and inserts on the lateral side of the squamosal, supratemporal and parietal.

2- Clavicle dorsalis

Originates from the muscle fascia of longissimus capitis 2 (plate 6.1.2d), and inserts on the anterior margin of the clavicle ventrally.

3- Levator scapula dorsalis and ventralis

Both muscles originate from the atlas (see chapter 1), and insert on the anterior side of the suprascapula.

4- Ribs to suprascapula/scapulocoracoid muscle slips

The superficial muscle slips originate from the distal end of the first, second, and third cervical ribs, and insert on the dorsal edge of the suprascapula. The fourth and fifth cervical ribs and first, second, third and fourth dorsal rib muscle slips insert on the posterior edge of the suprascapula. The deep muscle slips originate from the third and fourth cervical ribs, and insert on the suprascapula deep to the superficial slips (plate 6.1.3a).

Deep muscles

1- Obliquus capitis (externus and internus)

The obliquus capitis internus originates from the neural spine of C2, while the externus comes from the neural spines of C2-8 (plate 6.1.3b). Both muscles run anteriorly to insert on the lateral side of the paroccipital process (internus), or the paroccipital process, supratemporal, and lower edge of the parietal below the longissimus capitis 2 insertion (externus).

2- Rectus capitis (externus and internus)

The rectus capitis externus and internus originate from C1-2 and C1, and insert on the supraoccipital.

3- Splenius capitis

Originates superficially from the posterior neural spines C6-8, and extends anteriorly to insert on the mid-posterodorsal process of the parietal (tendinous bundle).

4- Spinalis and semispinalis muscles

a,b) Spinalis/ semispinalis cervicus and complex

See chapter 1.

5- Longissimus muscles

a) Longissimus dorsi

The muscle has slips from the zygapophyses (see chapter 1), and also from the spines of the dorsal vertebrae (D1, D2, D3.... etc).

b) Longissimus cervicus

See chapter 1.

c) Longissimus capitis 1

Branches from the longissimus dorsi (along the anterior cervical vertebrae), and inserts on the posterodorsal edge of the parietal done to mid-posterior process.

d) Longissimus capitis 2

Branches from the longissimus dorsi, and inserts on the supratemporal and ventral side of the parietal.

e) Longissimus capitis 3

Absent.

f) Longissimus capitis 4

Branches laterally from the longissimus dorsi, and inserts anteriorly on the basal tubera.

g) Longissimus capitis minor

Extends from the longissimus cervicus (see chapter 1), and inserts on the basioccipital (plate 6.1.3c) (posterodorsal to the longissimus capitis 4 insertion).

6- Iliocostalis muscle

a, b) Iliocostalis cervicus and major

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from D2 centrum (middle) and D3 rib ligament (lateral), and extends anteriorly (as slips) by originating from the posterior central midline keel, centra and intercentra. The muscle inserts on the basal tubera (short tendinous sheet), and is divided into 3 portions, Fig. (6.1.1/a):

1- Lateral: originates as a series of muscle slips from the posterior rib ligaments of C6-D2 and runs under the middle portion.

2- Middle: originates as muscle slips from the anterior margin of the deep blade-like intercentra (4-6), and runs under the anterior portion (with a tendinous origin).

3- Anterior: originates internally from the apices of the intercentra (2-5).

b) Longus cervicus

Originates from the C7 rib ligament, and runs anteriorly as slips which start from the rib ligaments of C4-7 and transverse process of C3. The muscle inserts on the second intercentrum base (V-shape) and the third intercentrum (lateral crest), Fig. (6.1.1/b)

8- First intercentrum to basioccipital and oto-occipital (superficial and deep)

Both branches originate from the tip of the first deep intercentrum, and insert on the central area between the basal tubera (superficial branch) and

on the ventral end of the oto-occipital (curved ridge) (deep branch) (plate 6.1.3c).

9- Posterior (2-3) intercentral muscle slips to basioccipital and oto-occipital

Originate from the second and third intercentral apices. Ventrally they insert on the basioccipital (deep to the longus colli insertion) and the ventral end of the oto-occipital (curved ridge) superficial and lateral to the first deep intercentrum muscle insertion (plate 6.1.3c).

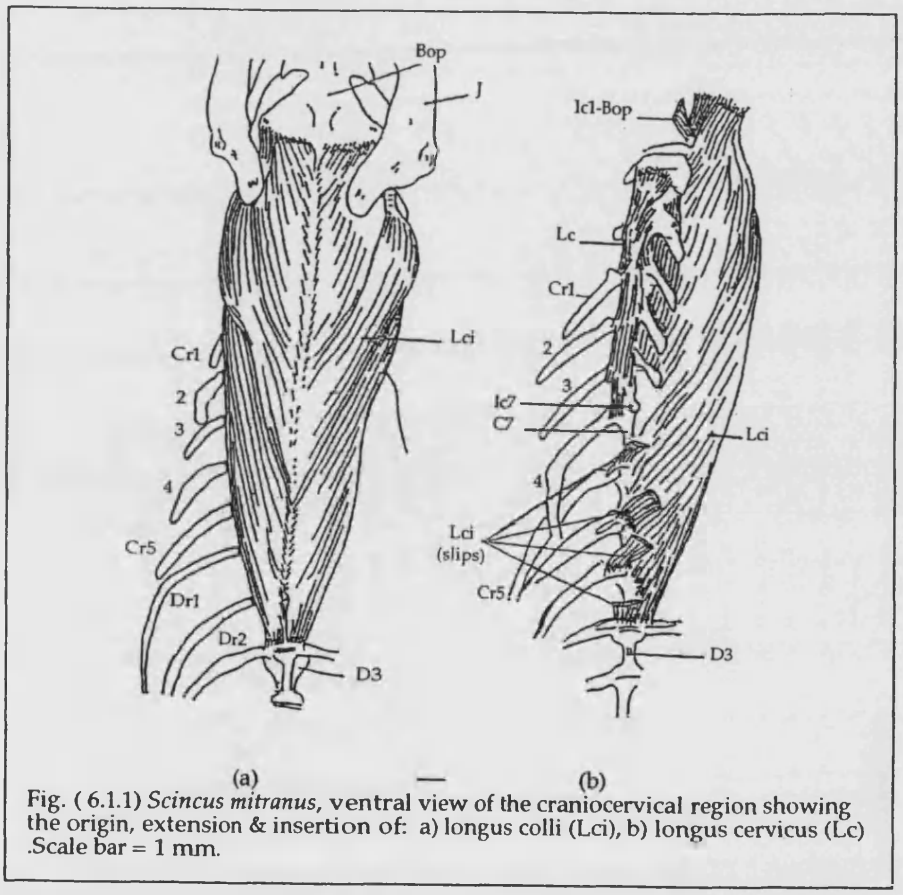


Fig. (6.1.1) *Scincus mitranus*, ventral view of the craniocervical region showing the origin, extension & insertion of: a) longus colli (Lci), b) longus cervicus (Lc) .Scale bar = 1 mm.

Very deep muscles

1- Deep intercentra to rib ligament muscle slips

The muscle originates from the posterior margins of the 2-5 intercentra, and inserts on the 1-4-rib ligaments.

2- Cervical and trunk central tendon

Absent.

- In *Scincus*, the episternocleidomastoid originates from the interclavicle, while in *Tiliqua* it originates from the interclavicle + sternum (tendinous).
- In *Scincus*, the rib to suprascapula muscle slips originate from the cervical and dorsal ribs D1 -4, while in *Tiliqua* the only dorsal slip is from D1.
- In *Tiliqua*, the obliquus capitis originates from the anterior cervical spines and inserts as one layer on the paroccipital process, while in *Scincus* it originates from the anterior + posterior cervical spines and inserts as two layers on the parietal and lateral skull components + paroccipital process.
- In *Tiliqua*, the splenius capitis originates between C4-D2, while in *Scincus* the muscle originates from C6-8.
- In *Scincus*, the longissimus dorsi originates dorsally from the neural spines and laterally from the zygapophyses, while in *Tiliqua* it originates from the zygapophyses only (as in all examined taxa).
- In *Scincus*, the longissimus capitis 2 inserts on the parietal and supratemporal, while in *Tiliqua* it inserts on the parietal and paroccipital process (plate 6.1.4a).

- Longus colli

Muscles name	*Scincus*	*Tiliqua*
Longus colli origin	Dorsal centrum and rib ligament (muscle fibres)	Cervical **or** dorsal centrum and rib ligament (tendon + muscle fibres)
Longus colli division	3 sections	One bundle
Longus colli extension	Slips from middle of the centra.	Slips from lateral side of the centra
Longus colli insertion	Short tendinous sheet	Long tendinous sheet

Anatomy of the neck region in Cordylidae

The cordylid taxa dissected were *Cordylus polyzonus, Gerrhosaurus flavigularis* and *Cordylus warreni. Cordylus polyzonus* was dissected in more detail.

A skeleton of *Pseudocordylus microlepidotus* was examined.

Previous works:

Lécuru, 1968; Hoffstetter and Gasc, 1969.

Osteology of *Cordylus polyzonus*

(Plate 6.2.1)

Skull

1-Parietal

The mid-posterodorsal margin is extended posteriorly, and possesses two shallow concavities (where splenius capitis inserts). The posterolateral processes are long and wide (where depressor mandibulae externus originates; episternocleidomastoid and longissimus capitis 1 and 2 insert).

2-Squamosal

This curved splint-like bone is longer than the supratemporal (where depressor mandibulae internus originates and episternocleidomastoid inserts).

3- Supratemporal

This elongated narrow bone extends along the posterolateral process of the parietal and the lateral margin of the paroccipital process (where episternocleidomastoid and longissimus capitis 2 insert). It contacts the parietal, squamosal and quadrate.

4- Quadrate

This is a wide bone with a posterodorsal process that is slightly exposed (where depressor mandibulae internus originates).

5- Retroarticular process

A well developed process with a wide posterior end (where depressor mandibulae internus and externus insert).

6- Paroccipital epiphysis

Absent.

6- Supraoccipital

This has a high keeled midline ridge (where rectus capitis inserts).

7- Oto-occipital

The paroccipital process is narrow (where obliquus capitis and longissimus capitis 2 insert). The ventral end of the oto-occipital possesses a curved ridge near to the occipital condyle (where intercentral muscle slips to the oto-occipital insert) .

8- Basioccipital

The basal tubera have oval epiphyses (where longus colli and longissimus capitis 4 insert). The area between the processes possesses a linear ridge (where the superficial first intercentral muscle slip inserts).

Presacral vertebral column

1- Atlas

This possesses a short posterior process and a wide transverse process. The intercentrum is keeled (where the first intercentral to basioccipital and oto-occipital muscle slip originates).

2- Axis

The postzygapophysis is smooth and the transverse process is wide (plate 6.2.1a). The second intercentrum is keeled and lacks lateral crests. The third intercentrum is fused to C3.

3- C3-8

There are 8 cervical vertebrae, and there are 5 intercentra (plate 6.2.1b). The neural spines become tall on C7 (where the splenius capitis muscle slips originate). The tips are triangular (spinalis /semispinalis cervicus attached) and short. The anterior and posterior margins of the neural spines are smooth, but the former is curved while the latter is straight. The neural spines are inclined in relation to the centra (60°). The postzygapophyses are smooth and horizontal. Ventrally, the centra are keeled between the adjacent smooth intercentra (where longus colli and cervicus extend). Each intercentrum is fused to the centrum behind (Hoffstetter and Gasc, 1969).

4- Anterior dorsal vertebrae

The neural spines are long and have compressed tips.

5- Ribs

The rib ratio = 3+3+2. The first, second and third cervical ribs are wide and possess cartilaginous ends (where ribs to suprascapula and iliocostalis muscle slips attach). The fourth and fifth cervical ribs are long and pointed. The ribs are connected to the transverse processes by ligaments.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

The bone articulates with the suprascapula (where trapezius muscle inserts and clavicle dorsalis originates), Fig. (6.2.1).

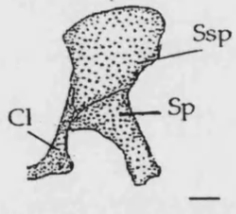


Fig. (6.2.1) *P. microlepidotus*, left lateral view of the pectoral girdle showing the clavicle (Cl) articulating with the suprascapula (Ssp). Scale = 1 mm.

3- Interclavicle

This cruciform bone has long narrow lateral arms (where episternocleidomastoid inserts), a long wide posterior arm and a short narrow anterior process (Lécuru, 1968).

4- Scapulocoracoid and suprascapula

A wide scapula that has a wide flat suprascapula.

Muscles of *Cordylus polyzonus*

(Plate 6.2.1 – 6.2.2)

Superficial muscles

1- Depressor mandibulae (internus and externus)

Originates from the quadrate and squamosal (internus), parietal and muscle fascia of longissimus capitis 1 (externus) (plate 6.2.1c). Both branches insert on the posterodorsal side of the retroarticular process (overlapping each other).

2- Cervicomandibularis

Originates dorsally on the muscle fascia of longissimus capitis 1 (plate 6.2.1c), and inserts on the articular (mandible).

3- Trapezius

Originates from the mid-dorsal line, and inserts on the suprascapula and clavicle.

4- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arms of the cruciform interclavicle (muscle fibres) and sternum (tendon) (plate 6.2.1e). It inserts wide on the supratemporal, squamosal and parietal (plate 6.2.2c).

2- Clavicle dorsalis

Originates ventrally from the muscle fascia of longissimus capitis 1 (plate 6.2.1d), and inserts on the anterior margin of the clavicle.

3- Levator scapula dorsalis and ventralis

Both muscles originate from the atlas transverse process and insert on the anterior margin of the suprascapula.

4- Ribs to suprascapula muscle slips

The first, second and third cervical rib muscle slips insert on the suprascapula superficially (dorsally), while the fourth and fifth cervical rib muscle slips insert on the suprascapula posteriorly (plate 6.2.1f). The second and third cervical rib muscle slips insert deep on the suprascapula (ventrally).

Deep muscles

1-Obliquus capitis

Originates from the dorsal end of the C2-4 neural spines, and inserts on the dorsal margin of the paroccipital process.

2-Rectus capitis

Originates from the dorsal end of C1-2 neural spines, and inserts on the dorsal edge of the supraoccipital.

3) Splenius capitis

Originates from C7-D1 neural spines, and inserts on the mid-posterodorsal process of the parietal.

4- Spinalis and semispinalis muscles

a) Spinalis capitis

Absent.

b, c) Spinalis and semispinalis cervicus and complex

See chapter 1.

5) Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches anteriorly and dorsally from longissimus dorsi, and inserts broadly on the dorsolateral side of the parietal (plate 6.2.2c).

c) Longissimus capitis 2

Branches anteriorly and dorsally from longissimus dorsi, and inserts laterally on the parietal, supratemporal and paroccipital process (L-shaped) (plate 6.2.2c).

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches laterally from the longissimus dorsi, and inserts on the lateral side of the basal tubera of the basioccipital (plate 6.2.2d).

f) Longissimus capitis minor

Branches from the longissimus cervicus ventrally, and inserts on the ventrolateral margin of the oto-occipital (dorsal to longissimus capitis 4) (plate 6.2.2b, d).

g) Longissimus cervicus

See chapter 1.

6- Iliocostalis muscles

a, b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from the posterior edge of the C7 centrum (medially) and the C8 rib ligament (laterally) (plate 6.2.2d), and extends anteriorly as a broad thick band (originating from the central midline). It inserts on the basal tubera via a tendinous bundle (starts along C5).

b) Longus cervicus

Originates from the posterior edge of the C5 centrum and C6 rib ligament, and originates from the centra, intercentra and rib ligaments. The muscle inserts on the base of the second intercentrum (V-shaped).

8- First intercentral muscle slip to basioccipital and oto-occipital (superficial and deep)

The first intercentrum muscle inserts on the central area of the basioccipital between the basal tubera (superficial), and on the curved ridge of the oto-occipital at the border with the basioccipital (deep).

9- Posterior (2-4) intercentral muscle slips to basioccipital and oto-occipital

Ventrally, the second, third and fourth intercentral muscle slips insert on the basioccipital deep to the longus colli insertion, and on the ventral end of the oto-occipital (curved ridge) superficial and lateral to the first deep intercentrum muscle insertion.

Very deep muscles

1) Cervical and trunk central tendon

Absent.

Comparison of osteological and muscular features within Cordylidae

A comparison of the neck anatomy between *Cordylus* (*Cordylus polyzonus* and *Cordylus warreni*), *Pseudocordylus microlepidotus* (skeleton) and *Gerrhosaurus flavigularis* shows similarities and variation:

1) Similarities between *Cordylus, Pseudocordylus* and *Gerrhosaurus*:

Excluding general similarities found in other lizards.

- Intercentra are fused to the centrum behind.
- Depressor mandibulae internus originates from squamosal and quadrate.

- Depressor mandibulae externus originates from the parietal (separate tendon bundle) and muscle fascia.
- Episternocleidomastoid inserts on the parietal, supratemporal and squamosal.
- Clavicle dorsalis originates from the muscle fascia of longissimus capitis 1.
- Longissimus capitis 2 inserts on the parietal, supratemporal and paroccipital process (L-shaped).
- Longissimus capitis 4 inserts ventrally on the basal tubera, while longissimus capitis minor inserts on the oto-occipital.

2) Variation between *Cordylus, Pseudocordylus* and *Gerrhosaurus*:

(Plate 6.2.3)

- In *Cordylus* median posterior process of the parietal extends as a single unit, but is forked in *Gerrhosaurus* and *Pseudocordylus*, Fig. (6.2.2).
- In *Gerrhosaurus*, the second intercentrum bears lateral crests, while in *Cordylus* and *Pseudocordylus* it is smooth.
- In *Gerrhosaurus*, most of the cervical intercentra bear two pairs of crests; basal (for rib ligaments), and lateral (longus cervicus attachment) crests, while in *Cordylus* and *Pseudocordylus* they are smooth, Fig. (6.2.3).

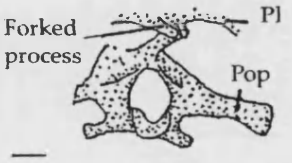


Fig. (6.2.2) *P. microlepidotus*, occipital view showing the parietal (Pl) is forked. Scale bar = 1 mm.

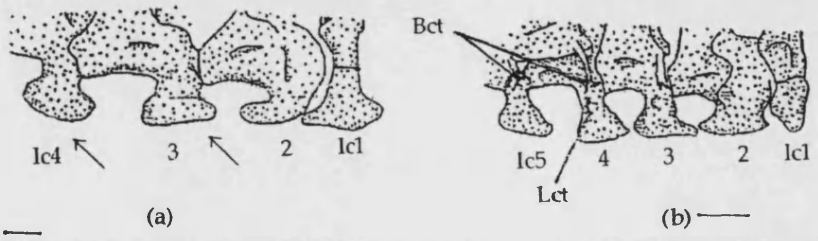


Fig. (6.2.3), Right ventrolateral view of the cervical vertebrae in; a) *P. microlepidotus*, where intercentra (Ic) lack crests, b) *G. flavigularis*, intercentra with basal & lateral crests (Bct & Lct). Scale bar = 1 mm.

- In *Gerrhosaurus*, there are 6 intercentra, but 4-5 in *Cordylus*, and 5 in *Pseudocordylus*.
- In *Gerrhosaurus*, the rib ligaments attach to the basal crests, while in *Cordylus* and *Pseudocordylus* they attach to the transverse processes.
- In *Gerrhosaurus*, the episternocleidomastoid originates from the interclavicle, while in *Cordylus* it originates from interclavicle and sternum.
- In *Gerrhosaurus*, the obliquus capitis originates as two layers, internus (C2) and externus (C2-6) (plate 6.2.3a), while in *Cordylus* it originates as one layer from anterior neural spines (plate 6.2.3b).
- Longus colli, longus cervicus and posterior intercentral muscle slips:

G. flavigularis	*Cordylus polyzonus & Cordylus warreni*
Longus colli Originates from C8 centrum (middle), and the D1 rib ligament (plate 6.2.3c) Narrow muscle Muscle fibres insert directly on the basal tubera by muscle fibres	Longus colli Originates from C7 centrum (posterior) and the C8 rib ligament Thick muscle Inserts on the basal tubera by a tendinous band
Longus cervicus Originates from C7 centrum (anterior) and the rib ligament.	Longus cervicus Originates from C5 centrum (posterior), and the C6 rib ligament.
Posterior intercentral muscles The 2-3 intercentral muscle slips insert on the oto-occipital.	Posterior intercentral muscles The 2-4 intercentral muscle slips insert on the basioccipital and the oto-occipital.

Anatomy of the neck region in Lacertidae

The lacertid taxa dissected were *Lacerta trilineata* and *Acanthodactylus boskianus asper*, with *Lacerta lepida pater* (skeleton). *Lacerta trilineata* was dissected in more detail. A skeleton of *Lacerta lepida pater* was also examined.

Previous works:

Lécuru, 1968; Hoffstetter and Gasc, 1969; Barbadillo and Barahona, 1994.

Osteology of *Lacerta lepida*

(Plate 6.3.1)

Skull

1- Parietal

The mid-posterodorsal margin is smooth, and the bone possesses two long wide posterolateral processes (where depressor mandibulae internus originates; episternocleidomastoid and longissimus capitis 2 insert).

2- Squamosal

This is a curved splint-like bone (where depressor mandibulae internus originates). It does not meet the paroccipital process.

3- Supratemporal

This wide elongated bone extends along the posterolateral process of the parietal and the paroccipital process (where the episternocleidomastoid inserts). It also contacts the squamosal and quadrate.

4- Quadrate

This is wide bone with a posterodorsal process that is slightly exposed (where depressor mandibulae internus originates).

5- Retroarticular process

This is a well-developed process with a pointed posterodorsal end (where depressor mandibulae internus and externus insert).

6- Supraoccipital

This has a high keeled midline ridge (plate 6.3.1a).

7- Oto-occipital

The paroccipital process is wide. The ventrolateral end of the oto-occipital near the basal tubera is convex (where longissimus capitis 4 inserts). The ventral end of the oto-occipital adjacent to the basioccipital possesses a curved ridge (where the deep intercentral muscle slips insert).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera have narrow elongated epiphyses. The area between the basal tubera possesses a linear ridge (where the first superficial intercentral muscle slip inserts).

Presacral vertebral column

1- Atlas

The posterior process is short and pointed dorsally. The transverse process is wide and the intercentrum is deeply keeled.

2- Axis

The postzygapophyses have tubercles and the transverse process is wide and projects strongly (where iliocostalis major attaches). Ventrally, the second intercentrum is keeled with lateral crests (plate 6.3.1d), while the third intercentrum is fused to C3.

3- C3-8

There are 8 cervical vertebrae and 8 keeled intercentra (7 cervical vertebrae in adult females of *Psammodromus* and *Lacerta vivipara* - Barbadillo and Barahona, 1994) (plate 6.3.1c). The tips of the neural spines are bilaterally compressed with short dorsal ends. The anterior and posterior margins of the neural spines/arches are smooth and curved. Laterally, the central width of C3-4 and C8 are equal to the length, while in C5-7, the width is greater than the length. The postzygaphyses are smooth (C5-8), and may possess a posterior process (C2-4). The postzygapophyses are straight (C2-7), and become inclined posteriorly <90° (C8). Ventrally, the centra between adjacent intercentra are keeled and the intercentra are fused to the centrum

behind (Hoffstetter and Gasc, 1969). The intercentra possess basal crests (plate 6.3.1d) (where the rib ligaments attach).

4- Anterior trunk vertebrae (dorsal vertebrae)

The neural spines are long and their tips are bilaterally compressed. The anterior margins are curved with a blade-like crest, and the posterior margins are straight.

5- Ribs

The rib ratio = 3 + 3+ 2 (plate 6.3.1c). The distal ends of the cervical ribs are wide with cartilaginous ends (where ribs to suprascapula and iliocostalis muscle slips attach). All cervical ribs have ligaments that connect them to the adjacent intercentra.

Pectoral girdle

1- Sternum

Well developed (plate 6.3.1b).

2- Clavicle

Well-developed bone that articulates with the suprascapula (where trapezius inserts).

3- Interclavicle

A cruciform bone with long narrow lateral anterior and posterior processes (where episternocleidomastoid originates) (plate 6.3.1b) (Lécuru, 1968).

4, 5- Scapulocoracoid and suprascapula

The scapula is wide and carries a large, curved flat suprascapula.

Muscles of *Lacerta trilineata*

(Plate 6.3.2 – 6.3.3)

Superficial muscles

1- Depressor mandibulae (internus and externus)

Originates from the quadrate, squamosal and parietal as muscle fibres (internus), and from the muscle fascia of longissimus capitis 2 (externus). Both branches insert on the posterior side of the retroarticular process (overlapping each other).

2- Cervicomandibularis

Originates from the muscle fascia of longissimus capitis 2, and inserts on the articular (mandible).

3- Trapezius

Originates from the mid-dorsal line (plate 6.3.2a), and inserts on the clavicle and suprascapula.

4- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arms of the interclavicle (muscle fibres) and the anterior side of the sternum (tendon), and inserts on the supratemporal and parietal.

2- Clavicle dorsalis

Originates from the muscle fascia of longissimus capitis 1, and inserts on the anterior margin of the clavicle (plate 6.3.2b).

3- Levator scapula dorsalis and ventralis

Both branches originate from the atlas transverse process and insert on the middle external surface (dorsalis) and the lower anterior margin (ventralis) of the suprascapula (plate 6.3.2b).

4- Rib to suprascapula muscles

The superficial first, second and third cervical rib muscle slips insert on the suprascapula dorsally, while the fourth, fifth and first dorsal rib muscle

slips insert on the posterior margin of the suprascapula (where the muscle attachment is continuous posteriorly along D2, D3 and D4 ribs) (plate 6.3.2c). The deep third and fourth cervical rib muscle slips insert on the suprascapula (ventrally).

Deep muscles

1- Obliquus capitis

Originates from C2-4, and inserts on the dorsal edge of the paroccipital process.

2- Rectus capitis

Originates from C1-2, and inserts on the dorsal surface of the supraoccipital.

3- Splenius capitis

Originates from the neural spines of C7-D1 (tendons), and inserts on the mid-posterodorsal side of the parietal.

4- Spinalis and semispinalis muscles

a) Spinalis capitis

Absent.

b, c) Spinalis/semipsinalis cervicus, spinalis/semispinalis complex:

See chapter 1 (plate 6.3.3a, b).

5- Longissimus muscles

a) Longissimus capitis dorsi

See capter 1.

b) Longissimus capitis 1

Branches from the longissimus dorsi along the anterior cervical vertebrae and inserts on the parietal.

c) Longissimus capitis 2

Branches from the longissimus dorsi and inserts on the ventrolateral margin of the paroccipital process and the parietal (L-shaped) (plate 6.3.2d).

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches laterally and deep from the longissimus dorsi, and inserts on the ventrolateral tip of the oto-occipital (convex) near the basal tubera.

f) Longissimus capitis minor

Branches from longissimus cervicus, and inserts on the ventrolateral margin of the oto-occipital dorsal to longissimus capitis 4 (plate 6.3.2d).

g) Longissimus cervicus

See chapter 1.

6- Iliocostalis muscles

a,b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from the middle of D1 centrum (muscle fibres) (plate 6.3.5b), and extends anteriorly as slips which originate from the central midline and intercentra. It inserts on the basal tuberculum as a short wide tendinous sheet.

b) Longus cervicus

Originates from the anterior margin of C8 centrum and rib ligament, and extends anteriorly to insert deep as slips on the intercentral base, centra and lateral rib ligaments (plate 6.3.5d). The last slip ends on the lateral base of the second intercentrum (V-shape).

8) First intercentral muscle slip to basioccipital and oto-occipital (superficial and deep)

The superficial branch of the first intercentral muscle inserts on the central area of the basioccipital between the basal tubera (linear ridge). The deep branch inserts on the ventral end of the oto-occipital(curved ridge) near the occipital condyle.

9) Posterior (2-4) intercentral muscle slips to basioccipital and oto-occipital

Ventrally, the second and third intercentral muscles insert on the basioccipital deeper to the longus colli insertion, while the deep third and fourth intercentral muscle slips insert on the ventral end of the oto-occipital (curved ridge) superficial and lateral to the first deep intercentral muscle insertion.

Very deep muscles

10) Cervical and trunk central tendon

Absent.

Comparison of osteological and muscular features within Lacertidae

A comparison of the neck anatomy between *Lacerta* (*Lacerta trilineata* and *Lacerta lepida pater* [skeleton]) and *Acanthodactylus boskianus asper* shows similarities and variation:

1) Similarities between *Lacerta* and *Acanthodactylus*:

Excluding general similarities found in other lizards.

- Intercentra are fused to the centrum behind.
- Depressor mandibulae internus originates from the quadrate, squamosal and parietal, while externus originates from the muscle fascia.
- Episternocleidomastoid inserts on the parietal and supratemporal.
- Clavicle dorsalis originates from the muscle fascia.
- Longissimus capitis 2 inserts on the parietal and paroccipital process (L-shape).
- Longissimus capitis 4 and longissimus capitis minor insert on the oto-occipital.

- The number of intercentral muscle slips is 3.

2) Variation between *Lacerta* and *Acanthodactylus*:

(Plate 6.3.4 – 6.3.5)

- In *Lacerta*, the midline ridge of the supraoccipital is keeled; it is rounded in *Acanthodactylus*.
- In *Acanthodactylus*, the third intercentrum is sutured between C2-3, while in *Lacerta*, it is fused to C3 (plate 6.3.4a, b).
- In *Lacerta*, the number of intercentra is 7-8 (plate 6.3.4a), or 5~6 (plate 6.3.4b) in *Acanthodactylus* They retain lateral crests (*Lacerta*) (where the ligaments attach to the transverse process)., or lack crests (*Acanthodactylus*).
- In *Lacerta*, the distal end of the first, second and third cervical ribs are wide, but are forked in *Acanthodactylus*.
- In *Acanthodactylus*, the fourth and fifth cervical rib muscle slips insert on the suprascapula posteriorly. In *Lacerta*, there are also slips from the first, second, third and fourth dorsal ribs.
- In *Acanthodactylus*, the splenius capitis originates from C6-D3 (plate 6.3.4c), while in *Lacerta* it originates from C7-D1.
- In *Lacerta*, longissimus capitis 2 inserts on the parietal and paroccipital process, but in *Acanthodactylus* it inserts on the supratemporal as well (plate 6.3.4d).
- In *Lacerta*, the longus colli originates from the D1 centrum, and inserts on the basal tubera with a wide short tendon. In *Acanthodactylus*, it originates from the C8 centrum and inserts on the basal tubera via a long narrow tendon (plate 6.3.5a).

- In *Lacerta*, there are 8 keeled intercentra and the longus cervicus originates from the C7 centrum and C8 rib ligament, while in *Acanthodactylus*, there are 5 keeled intercentra and the muscle originates from the C5 centrum and C6 rib ligament (plate 6.3.5c).

Anatomy of the neck region in Teiidae

Two teiid taxa were dissected, *Ameiva ameiva* and *Kentropyx calcarata*, but *Ameiva ameiva* was dissected in more detail.

Previous work:

Lécuru, 1968; Hoffstetter and Gasc, 1969; Estes et al., 1988.

Osteology of *Ameiva ameiva*

(Plate 6.4.1)

Skull

1- Parietal

The mid-posterodorsal margin is smooth with long wide posterolateral processes.

2- Squamosal

This splint-like bone has a wide dorsal process (plate 6.4.1a) (Estes et al., 1988). The squamosal is longer than the supratemporal but does not meet the paroccipital process.

3- Supratemporal

This long narrow bone extends along the posterolateral process of the parietal and along the lateral margin of the paroccipital process. In addition, it contacts the squamosal and quadrate.

4- Quadrate

The posterodorsal process is slightly exposed.

5- Retroarticular process

A well developed pointed posterior process.

6- Supraoccipital

It has a keeled midline ridge.

7- Oto-occipital

The paroccipital process is wide. The ventrolateral tip is convex and thick (where longissimus capitis 4 inserts), and the ventral end of the oto-occipital near the basioccipital has a curved ridge (where the intercentral muscle slips insert).

8- Paroccipital and quadrate epiphysis

Absent.

9- Basioccipital

The basal tubera have elongated narrow epiphyses.

Presacral vertebral column

1- Atlas

The posterior process is short and the transverse process is pointed. The intercentrum is deeply keeled.

2- Axis

The postzygapophysis is horizontal and bears tubercles. The transverse process is wide and projects strongly (plate 6.4.1d). Ventrally, the centrum is keeled and the second intercentrum is smooth. The third intercentrum is fused to the centrum behind (C3).

3- C3-8

There are 8 cervical vertebrae, and 6 keeled intercentra. The height of the neural spines increases from C5-7, and then decreases after C8. The dorsal ends of the neural spines are short with compressed dorsal tips. The anterior and posterior margins of the spines are smooth and curved. The postzygapophyses are horizontal and smooth. Ventrally, the centra are

keeled between adjacent smooth intercentra. The intercentra are fused to the centrum behind (plate 6.4.1e) (Hoffstetter and Gasc, 1969; Estes et al., 1988).

4- Anterior trunk vertebrae (dorsal)

The neural spines are long with compressed dorsal tips. The anterior and posterior margins of the spines/arches are smooth and curved.

5- Ribs

Rib ratio 3+3+2. The distal end of the first cervical rib is pointed, while posterior cervical ribs have wide ends (where rib to suprascapula and iliocostalis muscle slips attach). The cervical ribs have cartilaginous ends and bear ligaments that connect the ribs to the transverse processes.

Pectoral girdle

1- Sternum

Well-developed (plate 6.4.1c).

2- Interclavicle

The cruciform interclavicle (Lécuru, 1968) has long narrow lateral arms and a long wide posterior stem. The anterior process is narrow and short (plate 6.4.1c).

3- Clavicle

This is perforated medially (plate 6.4.1b) and articulates with the suprascapula dorsally.

4, 5- Scapulocoracoid and suprascapula

The scapula is wide and bears a wide curved suprascapula (plate 6.4.1b).

Muscles in *Ameiva ameiva*

(Plate 6.4.2)

Superficial muscles

1- Depressor mandible (internus and externus)

Originates from the quadrate, squamosal and posterolateral process of the parietal (internus) (plate 6.4.2b), and the muscle fascia of longissimus capitis 1 (externus). Both branches extend ventrally to insert on the retroarticular process (overlapping each other).

2- Cervicomandibularis

Originates from the muscle fascia of longissimus capitis 1, and inserts on the articular.

3- Trapezius

Originates from the mid-dorsal line, and inserts on the suprascapula and clavicle.

4- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arm of the interclavicle (muscle fibres), and sternum (tendon). It inserts on the supratemporal and parietal (plate 6.4.2b).

2- Clavicle dorsalis

Originates from the muscle fascia of longissimus capitis 1, and inserts on the anterior margin of the clavicle.

3- Levator scapula dorsalis and ventralis

They originate from the atlas transverse process, and insert on the anterior margin of the suprascapula.

4- Ribs to suprascapula muscle slips

The first, second and third cervical rib muscle slips insert on the suprascapula dorsally (superficial), while the second and third cervical rib muscle slips insert on the suprascapula ventrally (deep). The fourth and fifth cervical rib muscle slips insert on the suprascapula posteriorly.

Deep muscles

1- Obliquus capitis

Originates from C2-4 neural spines, and inserts on the dorsal margin of the paroccipital process.

2- Rectus capitis

Originates from C1-2 neural spines, and inserts on the dorsal margin of the supraoccipital.

3- Splenius capitis

Originates from C7-D2 neural spines, and extends anteriorly as one trunk to insert on the mid-posterodorsal side of the parietal.

4- Spinalis and semispinalis muscles

a) Spinalis capitis

Absent.

b, c) Spinalis and semispinalis cervicus/complex

See chapter 1.

5- Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches from longissimus dorsi to insert widely on the parietal.

c) Longissimus capitis 2

Branches from the longissimus dorsi to insert on the parietal and the ventrolateral side of the paroccipital (L-shape) (plate 6.4.2c).

d) Longissimus capitis 3

Absent.

E) Longissimus capitis 4

Inserts laterally on the basioccipital and ventrolateral tip of the oto-occipital (convex).

f) Longissimus capitis minor

Inserts deeply on the ventrolateral margin of the oto-occipital dorsal to longissimus capitis 4 (plate 6.4.2c).

g) Longissimus cervicus

See chapter 1.

7-Iliocostalis muscles

a, b) Ilicostalis major and cervicus

See chapter 1.

8) Longus muscles

a) Longus colli

Originates from C8 centrum (medially), and the rib ligament of D1 (laterally). It runs anteriorly as one thick trunk by originating from the central midline (posteriorly), and then from the centra and intercentra further anteriorly to insert on the basal tubera (tendon) Fig. (6.4.1).

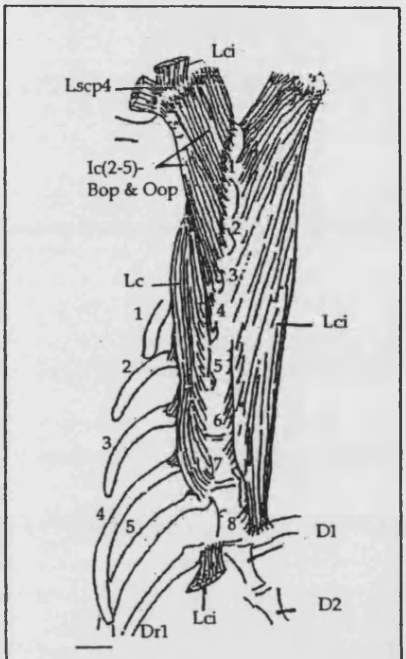


Fig. (6.4.1) *K. calcarata*, ventral view of the craniocervical region showing the longus colli (Lci) & cervicus (Ic) origin, extension & insertion where longus colli (Lci) >longus cervicus (Lc). Also intercentra 1-5 basioccipital and oto-occipital muscle slips (Ic[1-5]-Bop/Oop) and longissimus capitis 4 (Lscp4) insertion. Scale bar = 1 mm.

b) Longus cervicus

Begins from the posterior margin of C6 (plate 6.4.2d), and then extends anteriorly receiving slips from the centra, intercentra and rib ligaments. The muscle inserts on the second intercentrum base (V-shape).

9- First intercentral muscle slip to basioccipital and oto-occipital

The first intercentrum muscle inserts on the central area between the basal tubera (superficial branch), and on the curved ridge of the oto-occipital (deep branch).

10- Posterior (2-5) intercentral muscle slips to basioccipital and oto-occipital

The second and third intercentral muscle slips insert on the basioccipital (deep to the longus colli insertion), and on the ventral end of the oto-occipital (curved ridge). The fourth and fifth intercentral muscle slips insert on the oto-occipital only (lateral to the first deep intercentrum muscle insertion).

Comparison of osteological and muscular features within Teiidae

A comparison of the neck anatomy between two species; *Ameiva ameiva* and *Kentropyx calcarata* shows similarities and variation.

1) Similarities between *Ameiva* and *Kentropyx*:

Excluding general similarities found in other lizards.

- Long, curved squamosal with a wide dorsal process.
- Intercentra are fused to the centrum behind.
- Depressor mandibulae internus originates from the quadrate, squamosal and parietal.
- Depressor mandibulae externus originates from the muscle fascia of splenius capitis.
- Episternocleidomastoid inserts on the parietal and supratemporal.
- Longissimus capitis 2 inserts on the parietal and paroccipital process (L-shape).
- Longissimus capitis 4 inserts on the basioccipital and oto-occipital, while longissimus capitis minor inserts on the oto-occipital.
- The number of intercentral muscle slips is 4.

2) Variation between *Ameiva* and *Kentropyx*:

(Plate 6.4.2)

- In *Ameiva*, the clavicle dorsalis originates from the muscle fascia of longissimus capitis 1, while in *Kentropyx* the muscle originates from the parietal and muscle fascia (plate 6.4.2a).
- In *Ameiva*, the longus cervicus originates from the posterior edge of C6 centrum and rib ligament, while in *Kentropyx* the muscle originates from the posterior edge of C7 centrum and C8 rib ligament.

Comparison of osteological and muscular features within Scincomorpha

Table (6.5a) Osteology

Family / Bones features	Scincidae	Cordylidae	Lacertidae	Teiidae
Squamosal posterior end	Narrow			With dorsal process
Intercentral position	Fused to the centrum in front.	Fused to the centrum behind.		

Table (6.5b) Myology

Family / Muscle features	Scincidae	Cordylidae	Lacertidae	Teiidae
Origin of depressor mandibulae internus	Parietal, squamosal +/- quadrate	Squamosal & quadrate	Parietal, squamosal & quadrate	
Origin of depressor mandibulae externus	Parietal + muscle fascia		Muscle fascia	
Insertion of episterno-cleidomastoid	Parietal, supratemporal and squamosal		Supratemporal Parietal	
Insertion of longissimus capitis 2 on paroccipital process	Ventrally	L-Shaped, ventrolaterally		
Insertion of longissimus capitis minor	Basioccipital	Oto-occipital		
Number of posterior intercentral muscles	2	2 - 4	3	4

Common craniocervical features in Scincomorpha

Osteology

1- The ventral side of the oto-occipital near the occipital condyle bears a curved ventral ridge (**where posterior intercentral muscle slips insert**).

Myology

1- Depressor mandibulae internus attach to the quadrate.

2- Trapezius inserts on the suprascapula and clavicle (this character is shared uniquely with Gekkota).

3- Episternocleidomastoid inserts widely on the skull.

4- Deep rib to suprascapula muscle slips are present.

5- Spinalis capitis is absent.

6- Longissimus capitis 2 inserts mostly as (L – Shaped) on the paroccipital process.

7- The longus cervicus is shorter than the longus colli.

8- The first intercentral muscle slip inserts on the basioccipital (superficially), and oto-occipital (deep).

9- Ventrally, posterior intercentral muscle slips insert on the skull deep to longus colli and superficial and lateral to first intercentral muscle slip.

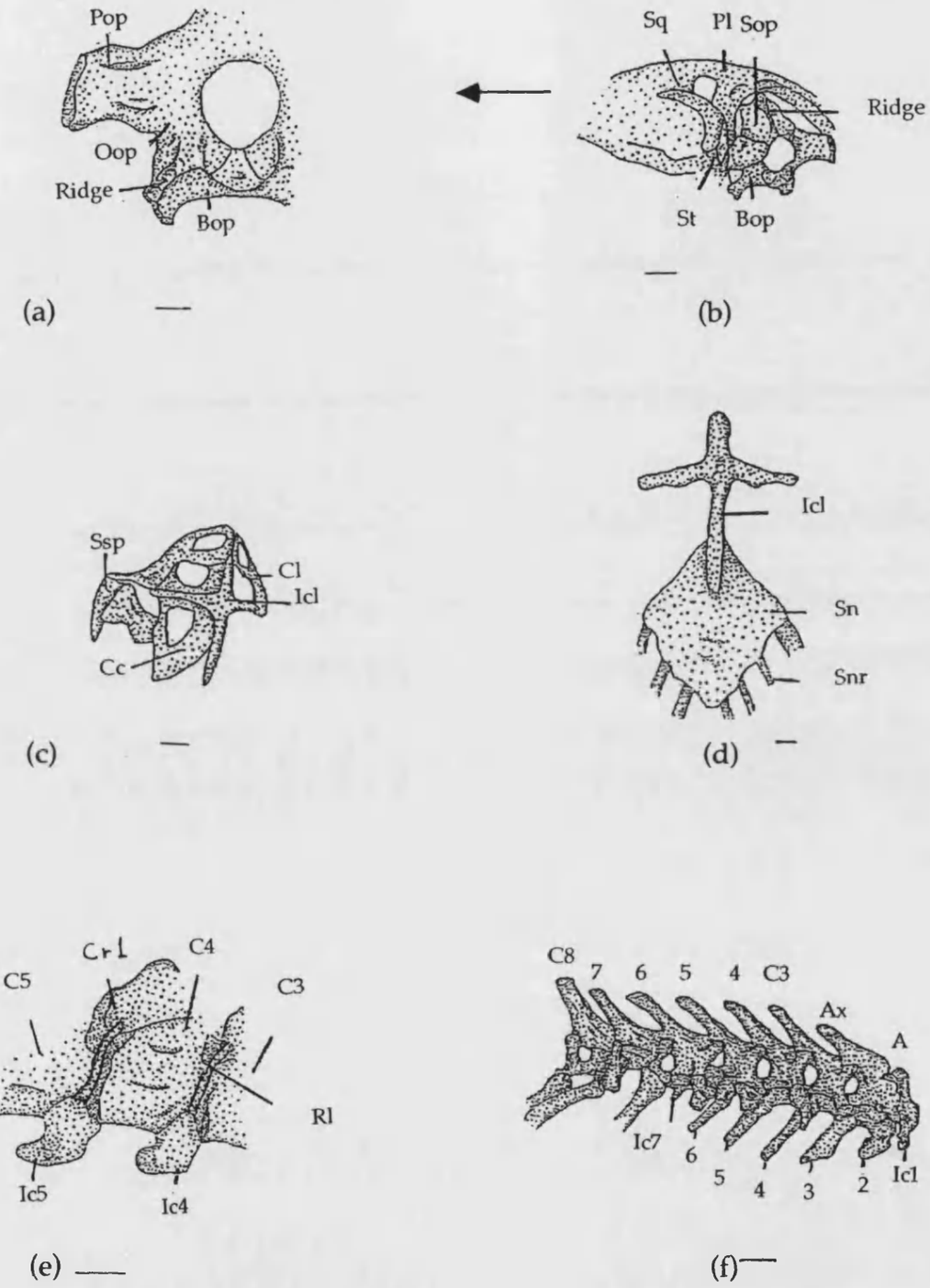


Plate (6.1.1) *Scincus fasciatus*, a) posterior view of the skull with ventrolateral ridge on the basioccipital (Bop); b) left posterolateral view of skull with supraoccipital (Sop) ridge; c-d) pectoral girdle ventral view with cruciform interclavicle (Icl) and perforate clavicle (Cl); e) right ventrolateral view of the cervical vertebrae with rib ligaments (RI) that connect intercentra to ribs (*S. fasciatus*); f) right lateral view of the cervical vertebrae with deep intercentra (Ic) (*S. mitranus*). Scale bar = 1 mm.

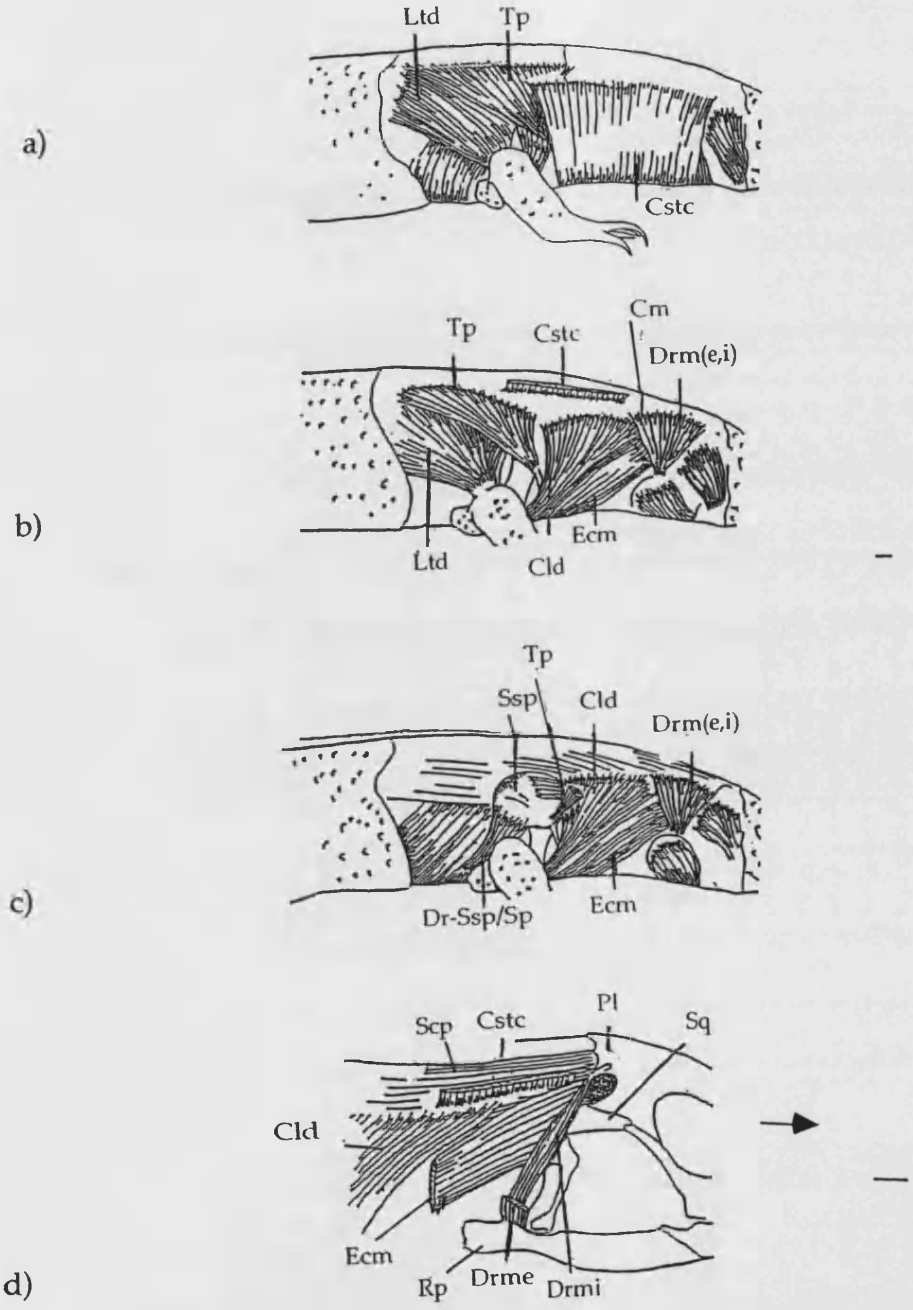
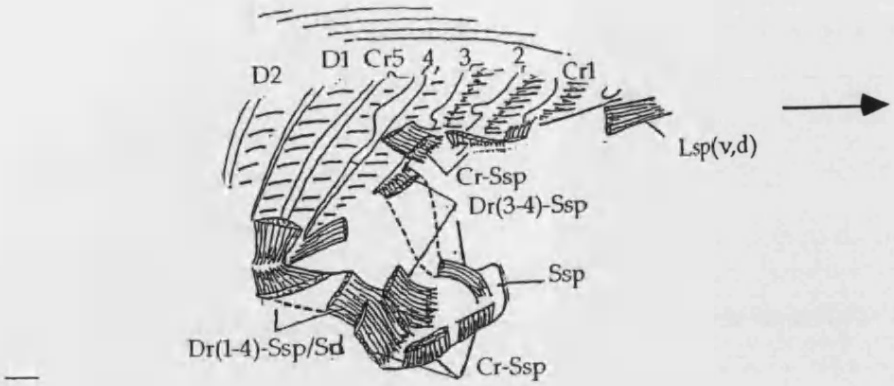
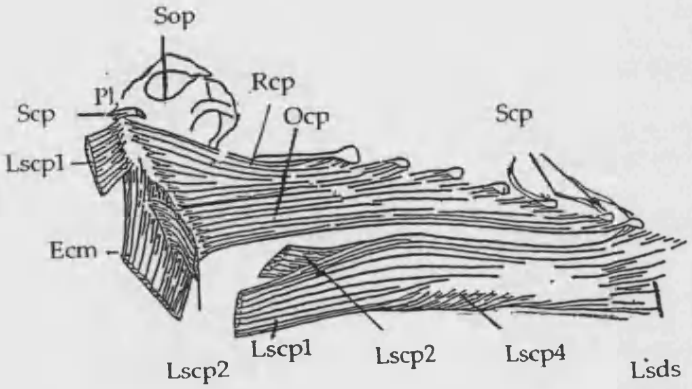


Plate (6.1.2) *S. mitranus* in right lateral view, a) superficial muscles including constrictor colli (Cstc); b, c) origin of trapezius (Tp), cervicomandibularis (Cm), latissimus dorsi (Ltd), clavicle dorsalis (Cld), episternocleidomastoid (Ecm) and depressor mandibulae (Drm); d) depressor mandibulae internus (Drmi) and episternocleidomastoid (Ecm) and the clavicle dorsalis (Cld) which inserts on the muscle fascia of splenius capitis (Scp). Scale bar = 1 mm.



(a)



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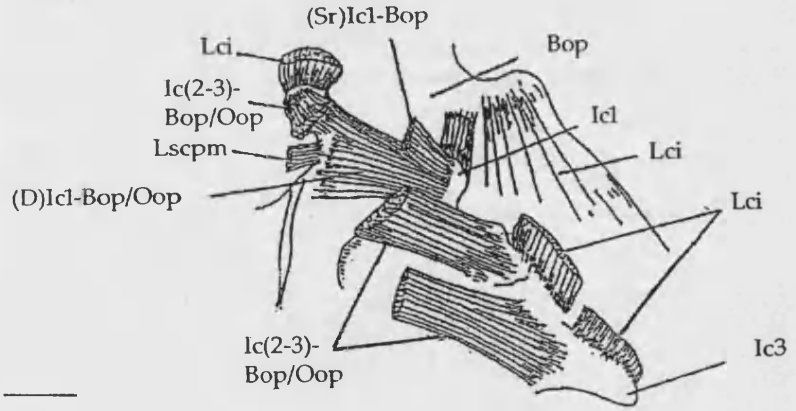
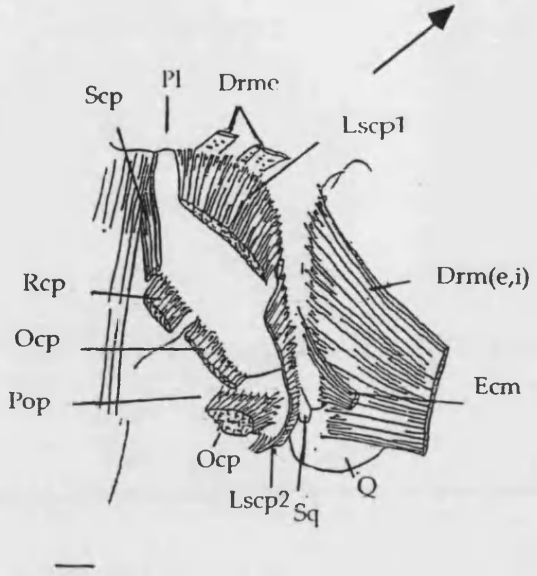
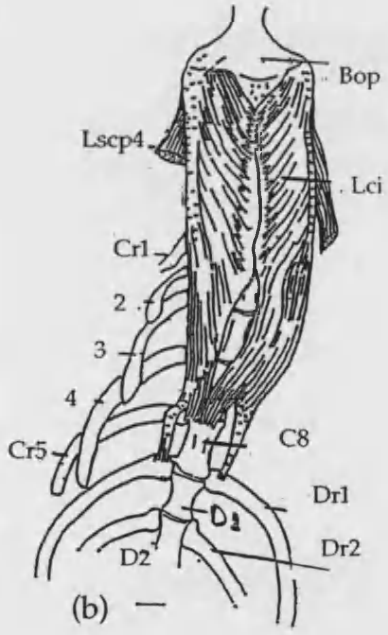


(c)

Plate (6.1.3) *S. mitranus*, a) right lateral view of the ribs showing cervical and dorsal rib to suprascapula muscle slips (Cr-Ssp, (D)Cr3-Ssp & Dr-Ssp/Sd); b) left dorsolateral view of craniocervical region showing the origin of the obliquus capitis (Ocp) from C2-8 and its insertion on the skull; c) left ventral view to show intercentral muscle slips to skull and deep first intercentral muscle slip ([D]Ic1-Bop/Oop), longus colli muscle slips (cut). Scale bar = 1 mm.



(a)



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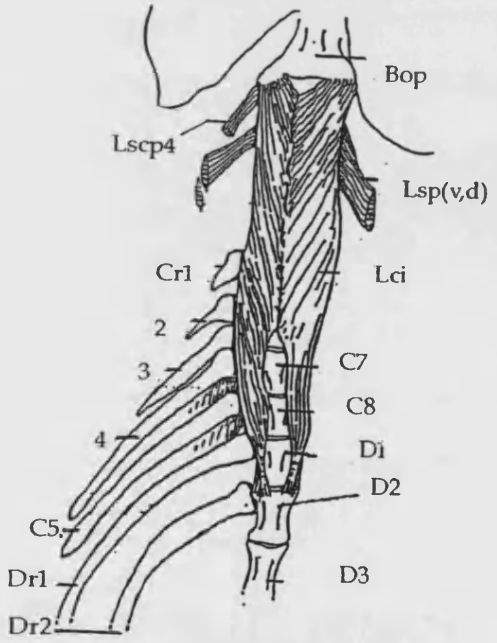


(c)

Plate (6.1.4) a) *Tiliqua nigrolutea*, posterior view of the skull showing, depressor mandibulae externus (Drme) originating from parietal, squamosal and quadrate (in *Scincus*, it originates from parietal and squamosal), episternocleidomastoid (Ecm) inserts on the parietal (in *Scincus*, from parietal, squamosal and supratemporal), longissimus capitis 2 (Lscp2) inserts on the parietal and paroccipital process (in *Scincus*, it inserts on supratemporal and parietal); ventral view of the craniocervical region showing, b) *T. rugosas* longus colli (Lci) originating from C8 and D1 rib, c) *T. nigrolutea*, longus colli (Lci) originating from D2 centrum ((in *Scincus*, it originates from D3 rib ligament). Scale bar = 1 mm.

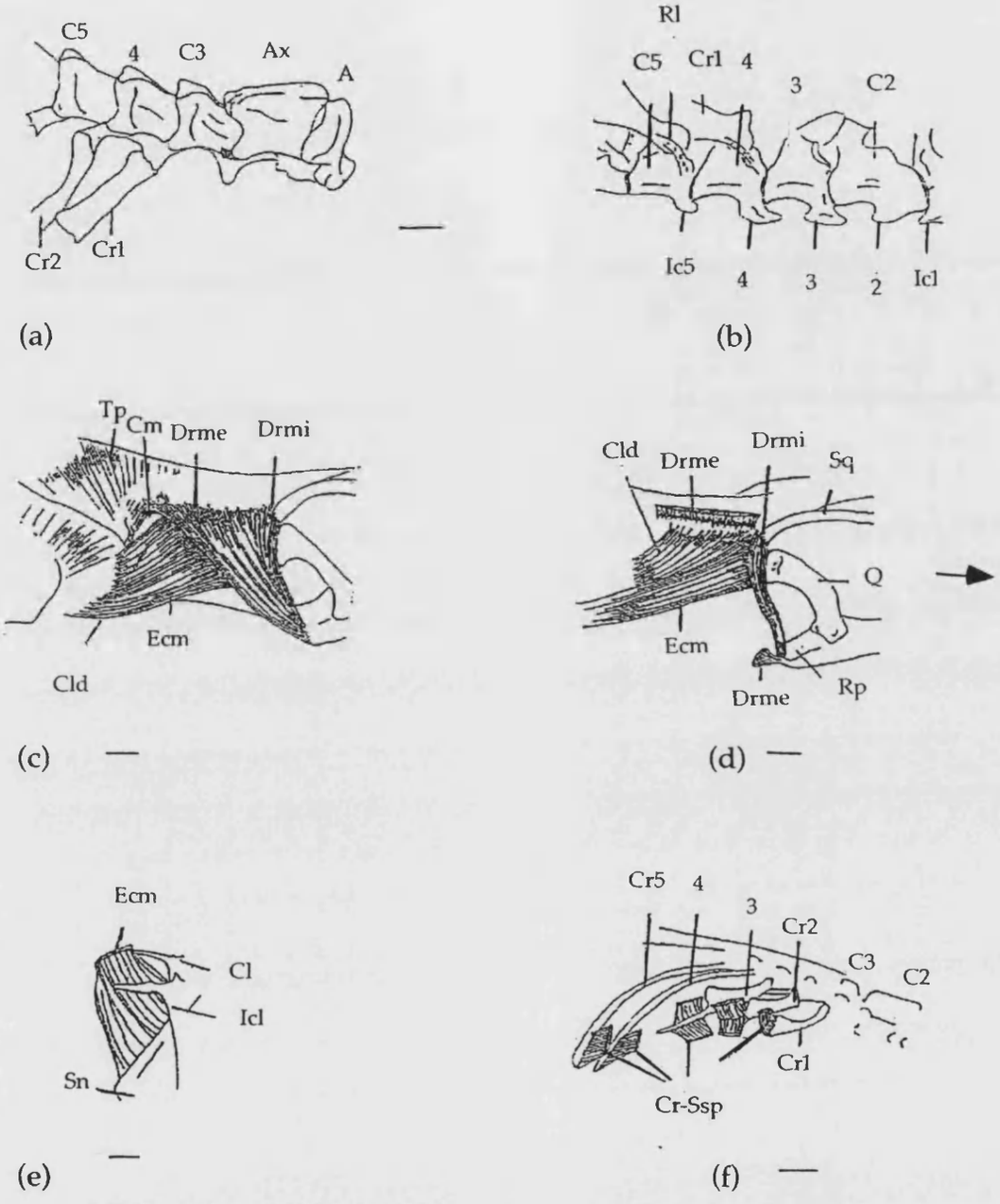


Plate (6.2.1) *Cordylus polyzonus,* a) right dorsolateral view of the anterior cervical vertebrae where first rib (Cr1) starts on C4; b) right ventrolateral view of cervical vertebrae with 5 intercentra (Ic) that are fused to the centrum behind. c) right lateral view of the neck showing the depressor mandibulae (Drm); d) right lateral view showing depressor mandibulae internus (Drmi) and clavicle dorsalis (Cld); e) partial left ventral view of pectoral girdle with episternocleidomastoid (Ecm) originating from interclavicle (Icl) and sternum (Sn); f) right lateral view of neck with cervical rib to suprascapula muscle slips (Cr-Ssp). Scale bar = 1 mm.

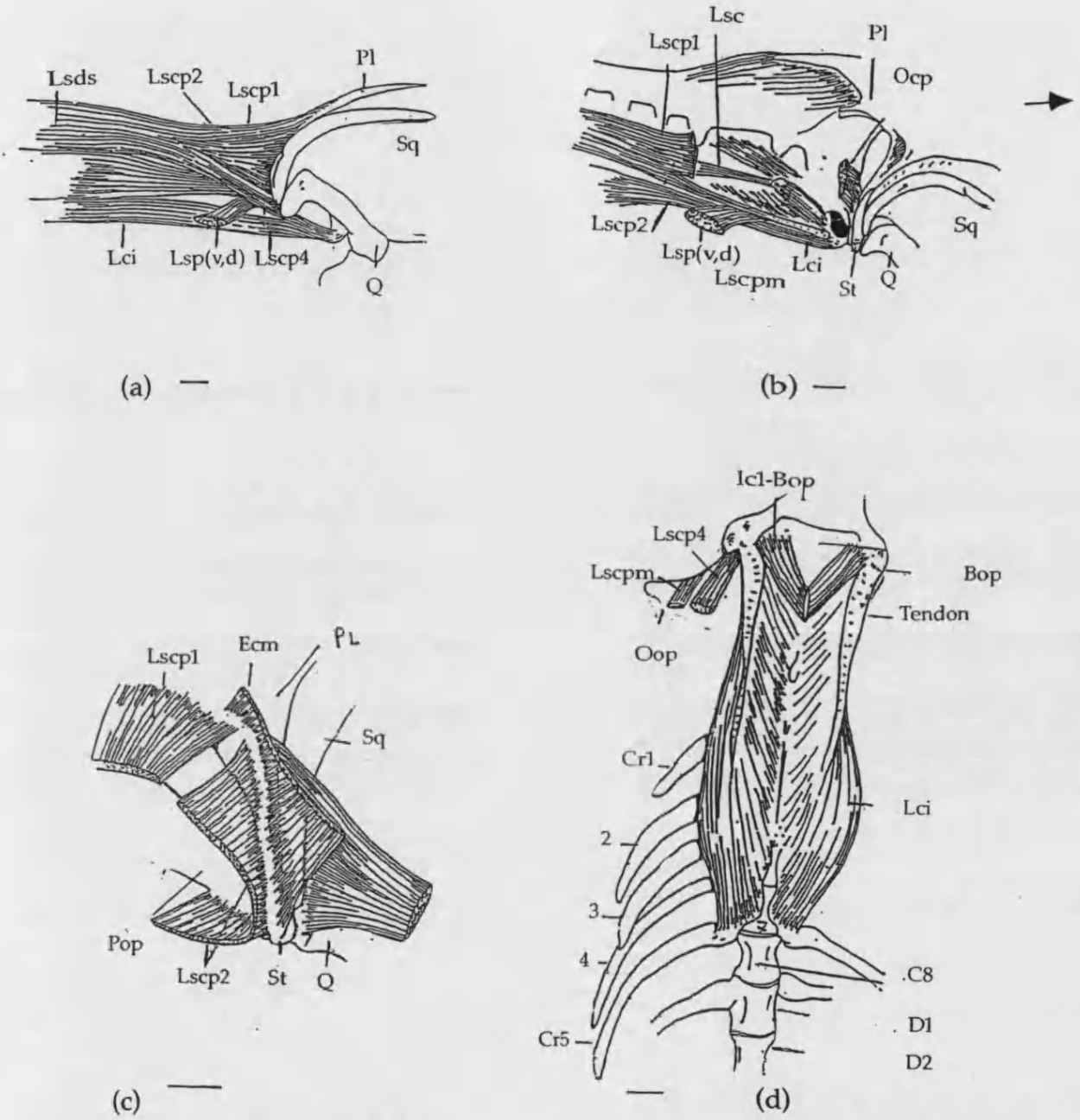


Plate (6.2.2) *Cordylus polyzonus*, a) right lateral view showing longissimus capitis 1, 2 and 4 (Lscp1,2 & 4) extension and insertion on the skull; b) right dorsolateral view showing longissimus capitis minor (Lscpm), levator scapula dorsalis and ventralis (Lspv & d) and longus colli (Lci) insertion; c) right side of skull in dorsal view showing insertion of episternocleidomastoid (Ecm) on supratemporal (St) and parietal (Pl), insertion of longissimus capitis 2 (Lscp2), supratemporal (St) and paroccipital process (Pop)); d) ventral view of the craniocervical region showing the origin of the longus colli (Lci) from C7 and C8 rib ligament. Scale bar = 1 mm.

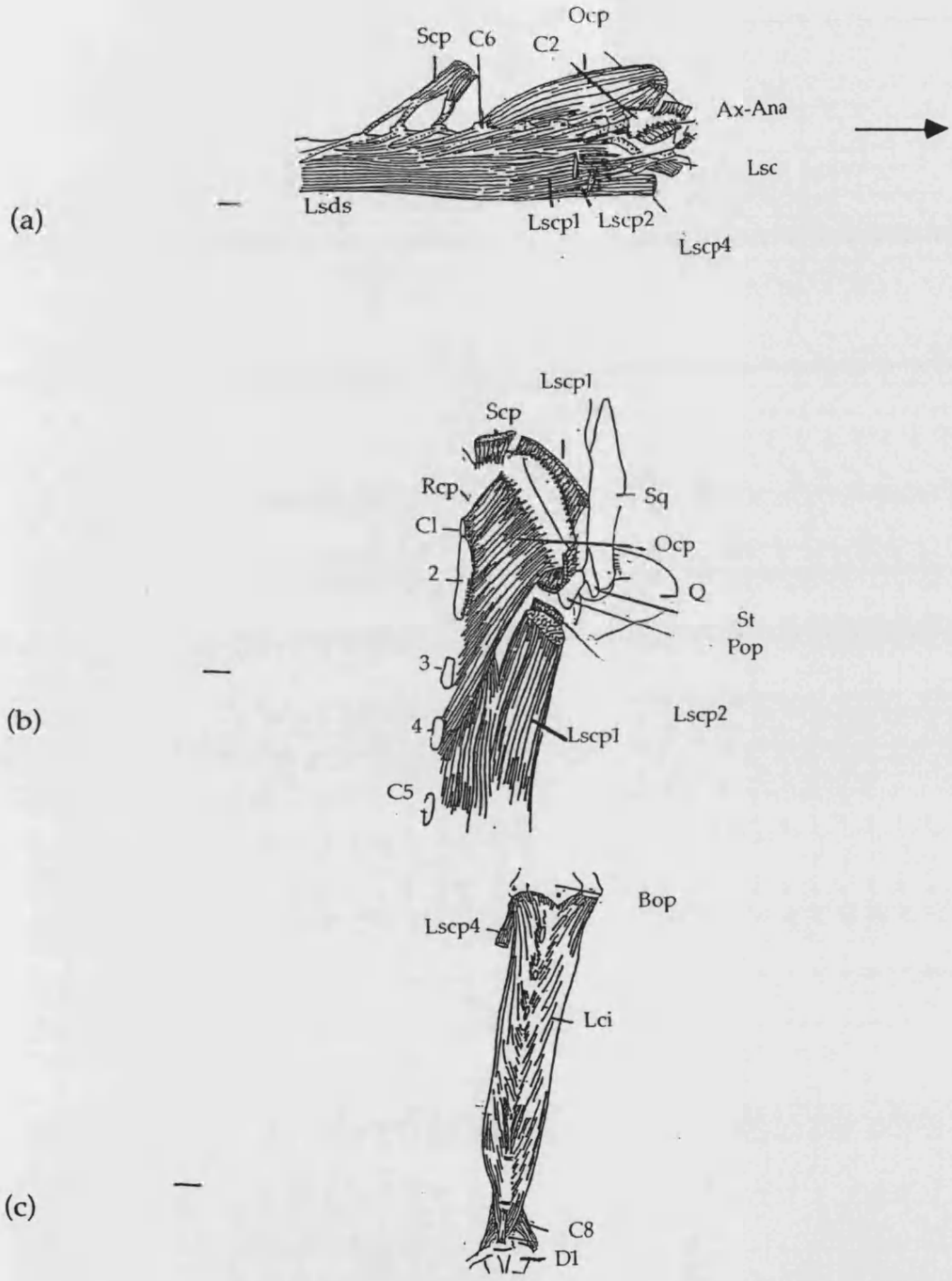
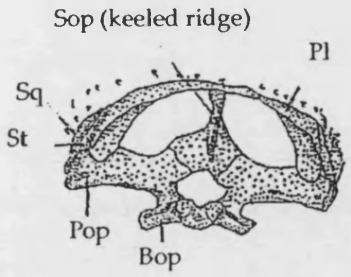


Plate (6.2.3) Cordylidae, a) right lateral view of the neck in *Gerrhosaurus flavigularis*, obliquus capitis originating from C2-6 (in *Cordylus*, from C2-4); b) dorsal view, right side, in *Cordylus warreni*, obliquus capitis (Ocp) originates from C2-4; c) ventral view of the neck muscles in *G. flavigularis*, longus colli (Lci) originates from D1 rib ligament (in *Cordylus* from C8 rib ligament). Scale bar = 1 mm.



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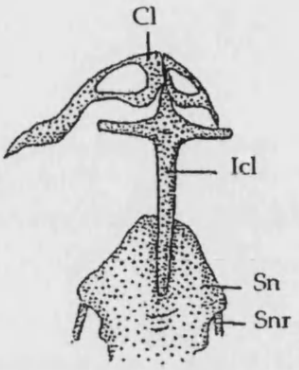

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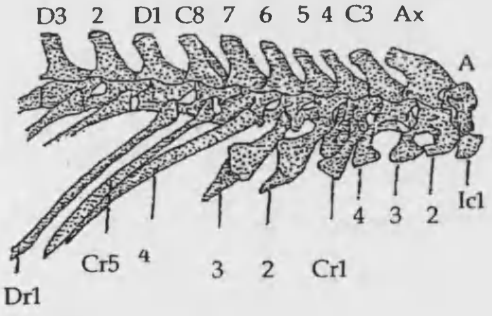

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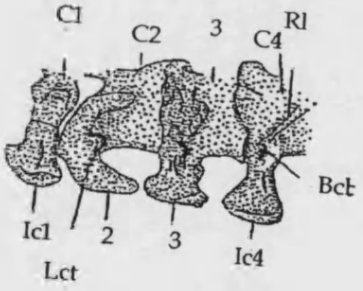
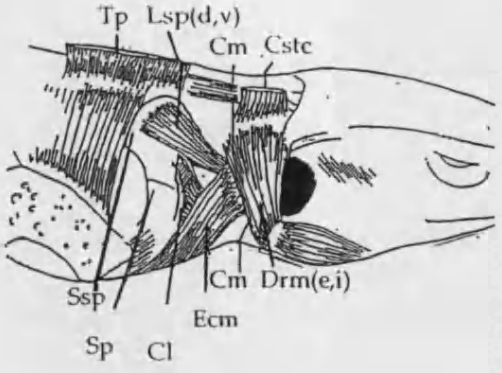


(d)

Plate (6.3.1) *Lacerta lepida*, a) occipital region of skull showing the keeled ridge of supraoccipital (Sop); b) ventral side of pectoral girdle showing perforate clavicle (Cl) and cruciform interclavicle (Icl); c) *L. lepida*, right lateral view of the cervical and dorsal vertebrae, rib ratio = 3+3+2; d) *L. lepida*, left lateral view intercentra (Ic) fused to the centrum behind, anterior intercentra with lateral and basal crests (Lct & Bct). Scale bar = 1 mm.



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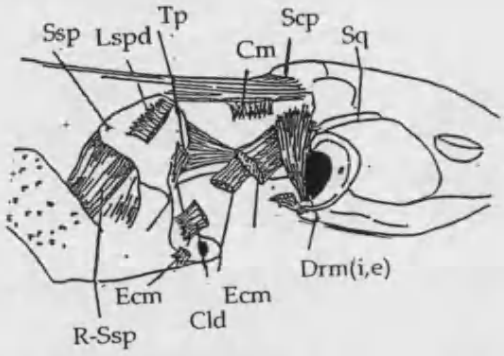

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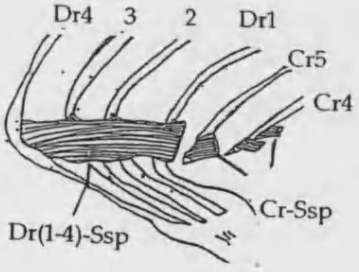
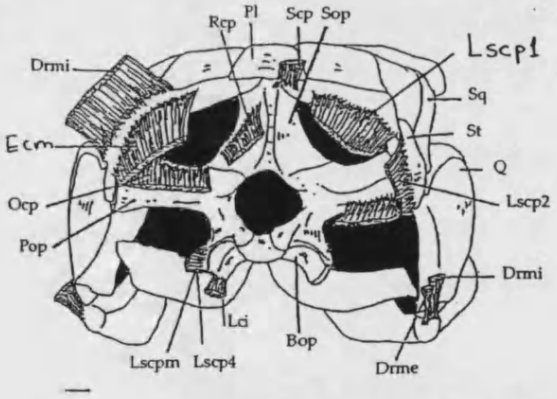
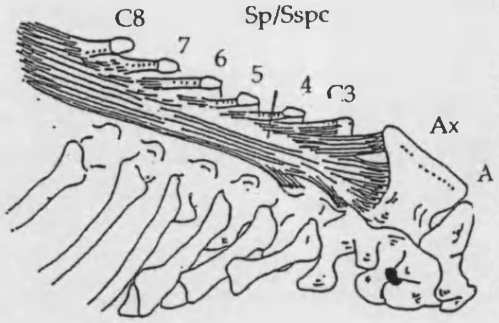




(c) (d)

Plate (6.3.2) *L. trilineata*, a) right lateral view of craniocervical region with most superficial and intermediate muscles including depressor mandibulae (Drme,i), cervicomandibularis (Cm) and trapezius (Tp); b) right lateral view showing clavicle dorsalis (Cld), episternocleidomastoid, and levator scapula dorsalis (Lspd); c) right ventrolateral view of dorsal rib to suprascapula ([Dr1-4]-Ssp) muscle slips; d) c) occipital view of the skull with most superficial, intermediate and deep muscle origin and insertions including longissimus capitis 2 (Lscp2) with L-shaped insertion on the paroccipital process (Pop) & parietal, episternocleidomastoid (Ecm) between the depressor mandibulae internus (Drmi) and longissimus capitis 1 (Lscp1), longus colli (Lci), and longissimus capitis 4 and minor (Lscp4 & m) on the oto-occipital Scale bar = 1 mm.

a)



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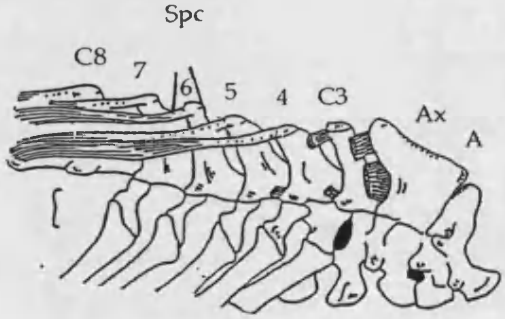

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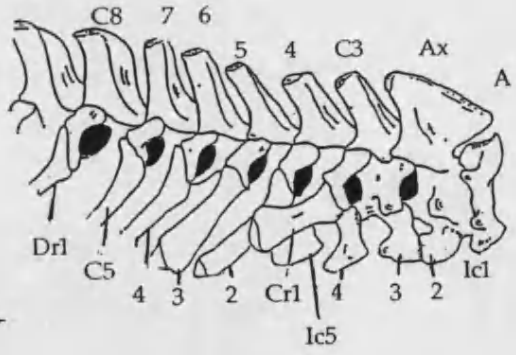
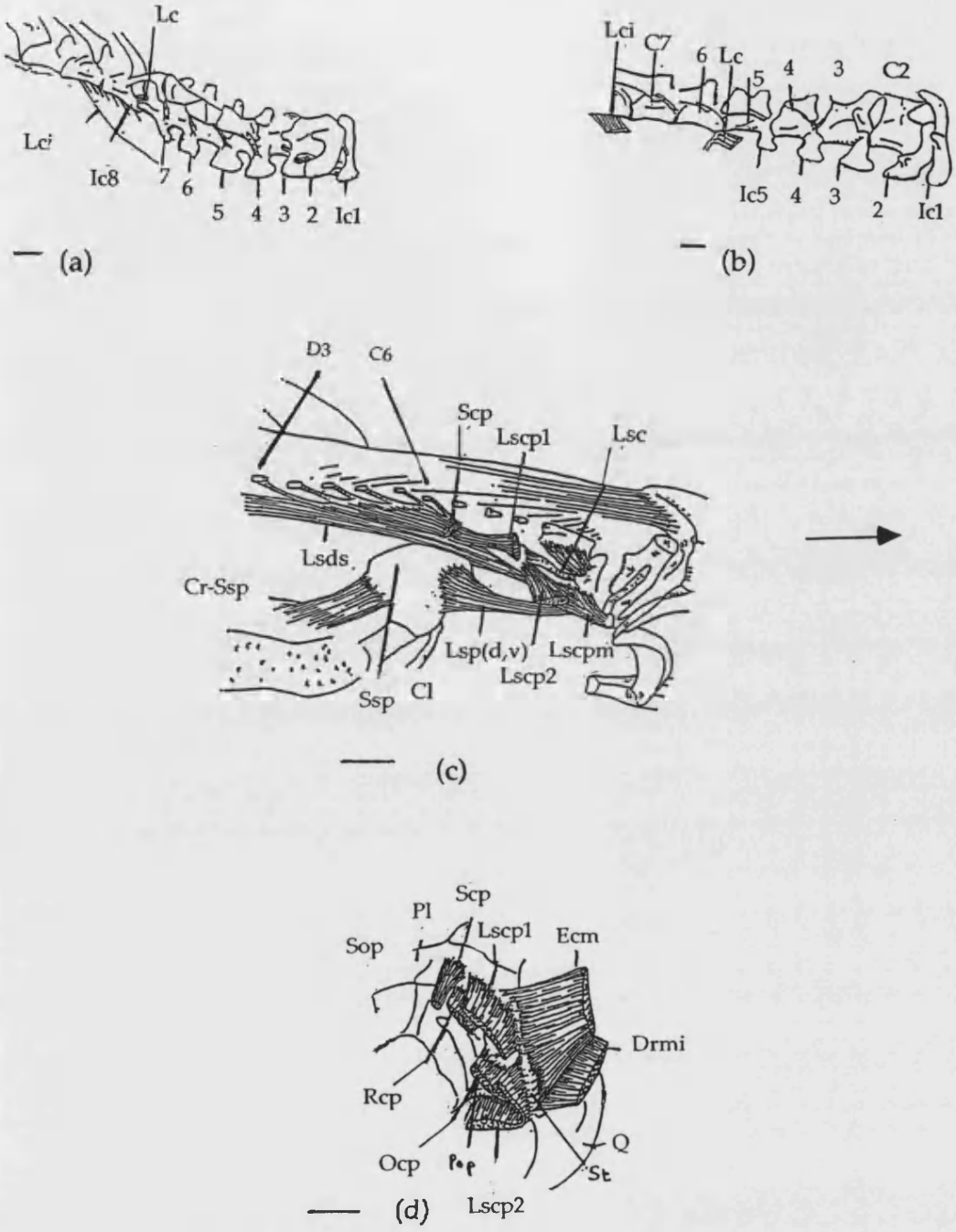


Plate (6.3.3) *L. trilineata*, right lateral view of the cervical vertebrae, a) spinalis and semispinalis cervicus (Sp/Sspc) attachment on the cervical vertebrae; b) spinalis slips (Spc) on the spines and arches of the cervical vertebrae; c) all muscles removed from the cervical vertebrae. Scale bar = 1 mm.



(d)

Plate (6.3.4) a) *Lacerta trilineata*, right ventrolateral view of cervical vertebrae showing number of intercentra (8); b) *Acanthodactylus boskianus asper*, right lateral view of cervical vertebrae showing number of intercentra (5); c) *Acanthodactylus boskianus asper*, right lateral view of craniocervical region showing splenius capitis (Scp) originating from C6-D3 neural spines (in *L. trilineata* it originates from C7-D1); d) *Acanthodactylus boskianus asper*, right occipital view of the skull where longissimus capitis 2 (Lscp2) inserts on the parietal (Pl), supratemporal (St) and paroccipital process (Pop) (while in *L. trilineata* it originates from paroccipital process and parietal). Scale bar = 1 mm.

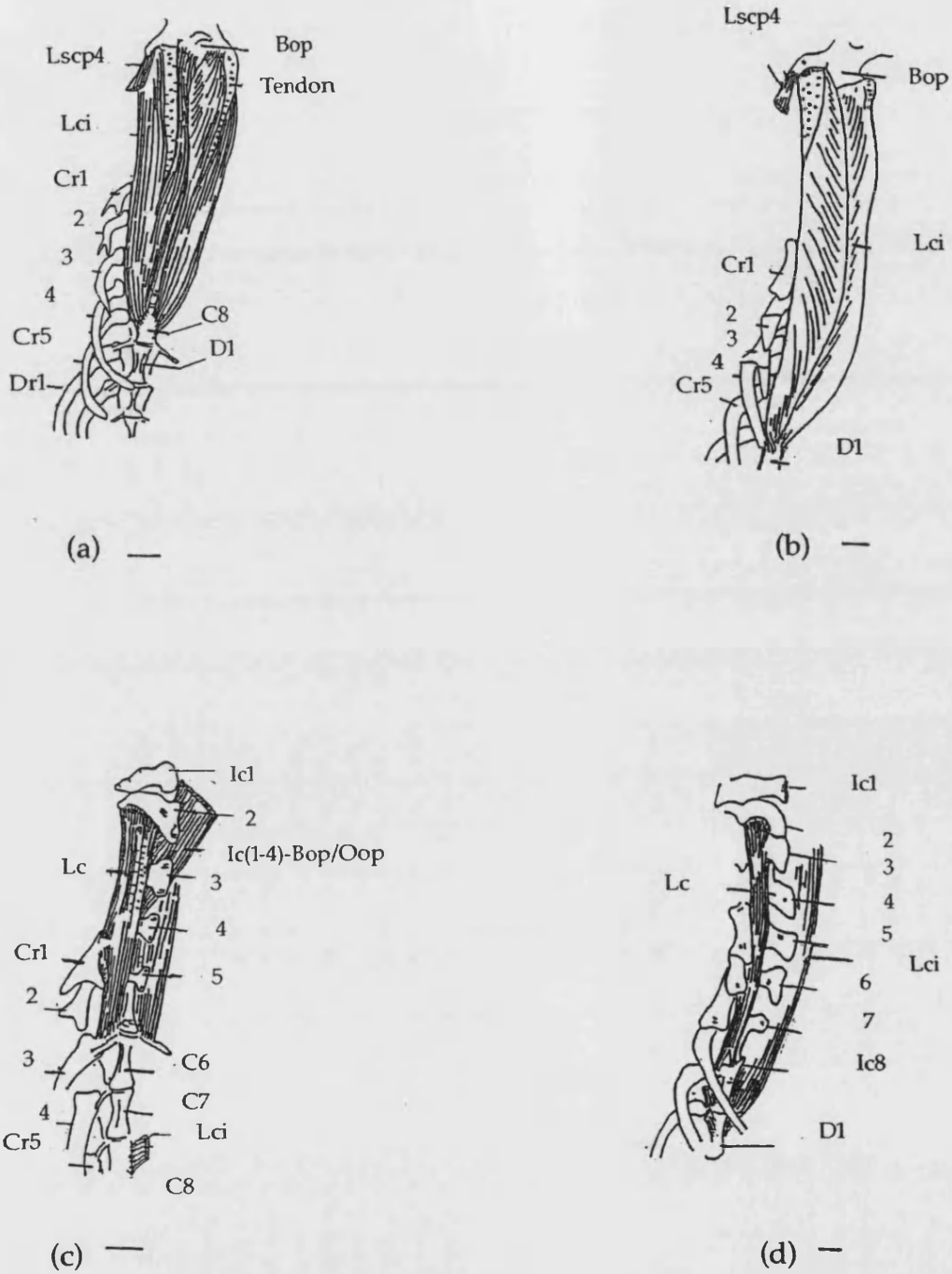


Plate (6.3.5) Ventral view of the neck region in a) *Acanthodactylus boskianus asper*, showing the origin of longus colli (Lci) from C8; b) *Lacerta trilineata*, showing the origin of longus colli (Lci) from D1; c) *A. b. asper*, origin of longus cervicus (Lc) from C6; d) *L. trilineata*, origin of longus cervicus (Lc) from C7 and C8 rib ligament. Scale bar = 1mm.

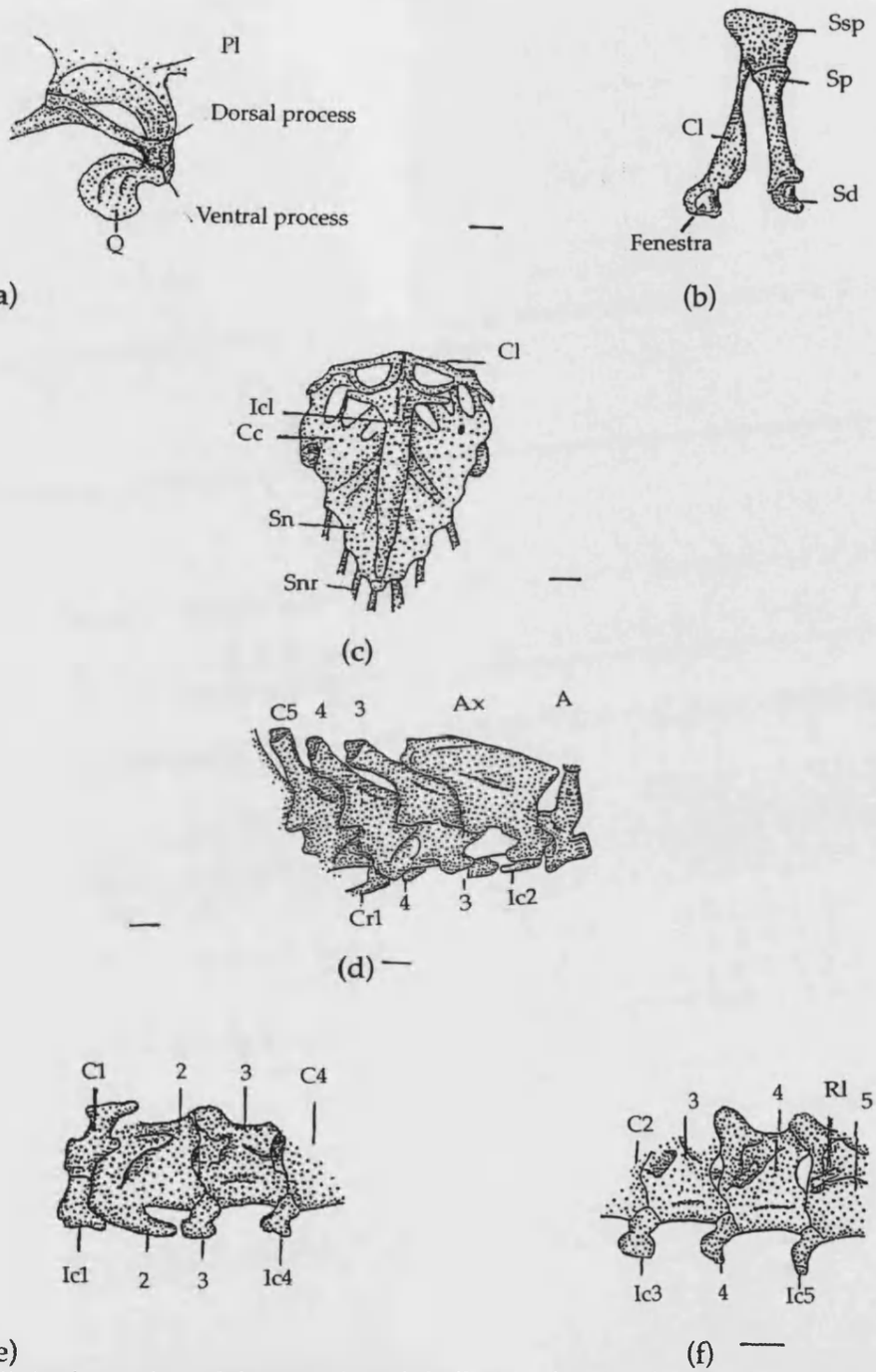


Plate (6.4.1) *Ameiva ameiva*, a) left posterolateral skull view showing dorsal and ventral processes of squamosal (Sq); b) left lateral view of pectoral girdle with fenestrated clavicle (Cl) which articulates with suprascapula (Ssp); c) ventral view of the pectoral girdle with cruciform interclavicle (Icl); d) right lateral view of the cervical vertebrae; e) left lateral view of anterior cervical vertebrae with keeled intercentra (Ic) (1-4); f) left lateral view of anterior cervical vertebrae showing keeled intercentra (3-5) which are fused to the centrum behind. Scale bar = 1 mm.

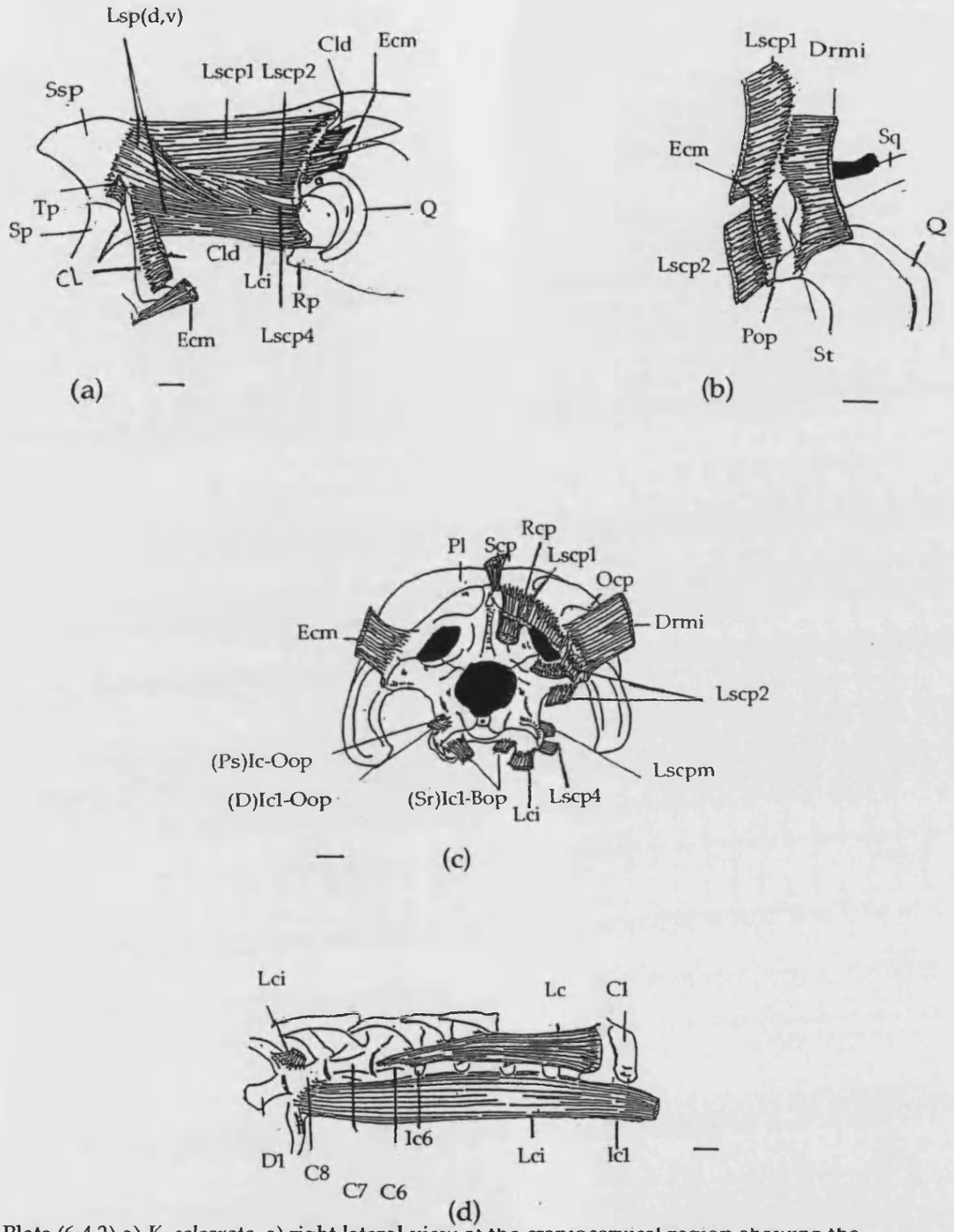
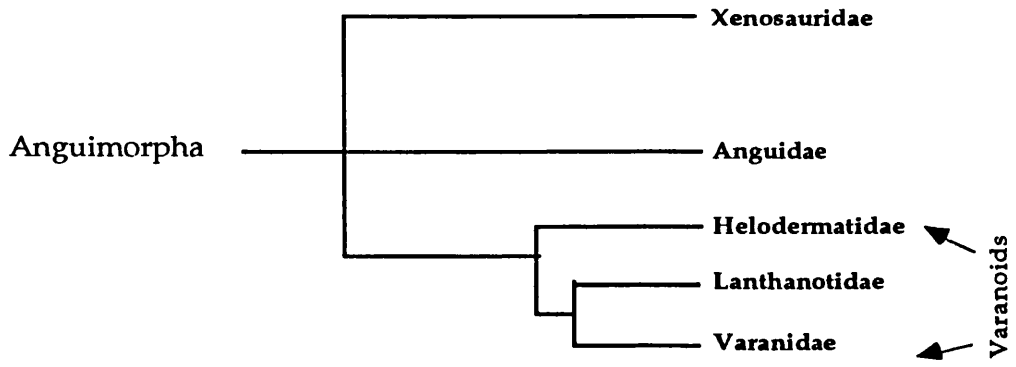


Plate (6.4.2) a) *K. calcarata*, a) right lateral view of the craniocervical region showing the clavicle dorsalis (Cld) originates from parietal (Pl) and muscle fascia. b) *Ameiva ameiva*, right posterolateral view of the skull with episternocleidomastoid (Ecm) inserting on supratemporal and parietal while depressor mandibulae internus (Drmi) originates from parietal, quadrate and squamosal; c) posterior view of the braincase showing the insertion of the longissimus capitis 2 (Lscp2) on the lateral and ventral edge of the paroccipital process, also the insertion of the superficial and deep first intercentral slips on the basioccipital and oto-occipital (Sr [Ic1-Bop] & D[Ic1-Oop) ; d) right ventrolateral view of cervical vertebrae where longus colli (Lci) originates from D1 rib ligament and longus cervicus (Lc) originates from C6. Scale bar = 1 mm.

CHAPTER (7)

ANGUIMORPHA

Anguimorphs are one of the primary groups of scleroglossans. This well recognized group is divided into 5 families: Anguidae, Helodermatidae, Lanthanotidae, Varanidae, and Xenosauridae (Halliday and Adler, 1986).



Family: Anguidae

This family includes about 100 species found throughout North America and Eurasia. The family contains both limbed and limbless forms, and their length ranges from 60 – 300 mm. Anguids have keeled scales with well-developed osteoderms.

The family includes 4 subfamilies: Anguinae, Anniellinae, Diploglossinae and Gerrhonotinae. The first two subfamilies contain limbless forms. The widely distributed anguines (e.g. slow worms) are the only anguid group to occur in the Old World. The limbs are reduced or lost, although the girdles remain and the tail is long, e.g. *Anguis fragilis.* Anniellinae contains a single genus *Anniella* with two species, from California. The limbed Diploglossinae (galliwasps) include 40 species and are skink-like animals. They have smooth overlapping scales and usually short legs, e.g. *Diploglossus crusculus.* In a few genera, the limbs may be further reduced e.g. the South American genus *Ophiodes.* The Gerrhonotinae (e.g. *Elgaria*) have well-developed limbs and are found over a range that extends from Southwest Canada to Central

America. There are about 40 species, which occupy a diversity of habitats (Webb et al., 1978; Halliday and Adler, 1986; Bauer, 1992; Zug, 1993).

Family: Helodermatidae

Helodermatids are large burrowing lizards that occupy the deserts of the southwestern United States through to northwestern Mexico and Guatemala. They are the only venomous lizards and have grooved teeth to carry poison from a series of labial glands. There is a single living genus and two species: the Gila monster (*Heloderma suspectum*) and the Mexican Beaded Lizard (*H. horridum)* (Webb et al., 1978; Halliday and Adler, 1986; Beck and Lowe, 1991; Bauer, 1992).

Family: Lanthanotidae

The family contains one living genus and species *Lanthanotus borneensis.* This lizard lives in the northern part of the island of Borneo, where it burrows and swims in small forest streams (using short well-developed limbs). The full length ranges up to 20 cm, and the tail is long and slender. This Earless Monitor is closely related to the true monitors of the family Varanidae (Webb et al., 1978; Bauer, 1992).

Family: Varanidae

The varanids include at least 48 species within a single living genus, *Varanus*. They are found across warmer parts of the Old World including Asia, Africa and Australia, but are absent in Madagascar. Monitor lizards have a distinctive short body with a long neck and a very long muscular tail. The head is long and narrow, and the limbs are well developed. Varanids are mostly carnivores but some are insectivorous (e.g. *V. olivacens,* Philippines). The length ranges from 1.2 – 3 m.. The largest is *V. komodoensis,* the Komodo dragon, which occupies the islands of Flores, Komodo and Padar. Most monitors are terrestrial, and/or partially aquatic but the

Emerald Tree Monitor, *Varanus prasinus*, is an arboreal species with a long tail, e.g. *V. mertensi* (Webb et al., 1978; Halliday and Adler, 1986; Bauer, 1992; Zug, 1993).

Family: Xenosauridae

The xenosaurids include 2 living genera and 5 species, four of which belong to *Xenosaurus* (Mexico and Guatemala), while *Shinisaurus crocodilurus* lives in Guanxi province, southern China. Xenosaurs have well-developed limbs and range in length from 100 - 150 mm. *Xenosaurus* lives in a variety of habitats although they prefer moist wet areas. *Shinisaurus crocodilurus* is a semi-aquatic lizard that occurs along lake and river margins where it feeds on fish, tadpoles and insect larva (Webb et al., 1978; Bauer, 1992; Zug, 1993).

Anatomy of the neck region in Anguidae

Members of the family Anguidae vary from limbed to limbless. I dissected one anguid with well-developed limbs as *Elgaria multicarinata*; one anguid with short limbs (*Diploglossus crusculus crusculus*; *D. monotropis* and *D. shamini* skeletons; two limbless anguids (*Ophiodes intermedius*; *O. striatus* skeleton and *Anguis fragilis*).

Previous works:

Parker, 1868; Camp, 1923; McDowell and Bogert, 1954; Hoffstetter and Gasc, 1969.

(A) Osteology of *Elgaria multicarinata* (anguid with well-developed limbs)

(Some osteological features were not investigated during dissection)

(Plate 7.1.1)

Skull

1- Oto-occipital

The ventrolateral tip of the oto-occipital is convex (plate 7.1.1c) (where the longissimus capitis 4 inserts). At the junction with the basioccipital, the oto-occipital bears a shallow ridge (for deep intercentral muscles).

2- Basioccipital

The basal tubera have elongated epiphyses (where longus colli inserts), and the area between the tubera bears a short sharp ridge (where the first intercentral muscle inserts).

Presacral vertebral column

1- Atlas

The posterior process is long, and the transverse process is pointed posteriorly. The intercentrum is keeled (where the first intercentral muscle slip originates).

2- Axis

The transverse process is pointed (where the iliocostalis major attaches). Ventrally, the anterior and posterior intercentra are smooth, and the second intercentrum is fused to C2.

3- C3-8

There are 8 cervical vertebrae, and 5 keeled intercentra (plate 7.1.1d). The height of the neural spines is constant anteriorly (C3-6), but increases posteriorly (C7-8). The tips of the spines are triangular with short dorsal ends. The anterior margins of the spines are smooth and curved, while the posterior margins are straight. The width of the arches is equal to the length. Ventrally, the anterior centra are smooth between the intercentra, becoming sharply keeled posteriorly on C5, less sharp on C6, and then rounded on C7. All intercentra are smooth except the fourth, which bears lateral crests (where the second rib tendon inserts = longus cervicus?). Each intercentrum is fused to the centrum in front.

4- Ribs

The rib ratio is 3+3+2. The distal ends of the cervical ribs are pointed and possess cartilaginous tips. The shafts are smooth and flat.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

It runs across the anterior margin of the scapulocoracoid to end dorsally on the suprascapula.

3- Interclavicle

This cruciform bone has long narrow lateral, posterior and anterior arms. The lateral arms are inclined to the horizontal (plate 7.1.1a) (Camp, 1923; McDowell and Bogert, 1954).

4, 5- Scapulocoracoid and Suprascapula

The scapulocoracoid is wide and bears a wide flat suprascapula.

Myology of *Elgaria multicarinata* (anguid with well-developed limbs)

(Plate 7.1.1)

Superficial muscles

1- Depressor mandibulae (internus and externus)

This originates from the quadrate and squamosal (internus), and from the supratemporal, parietal and muscle fascia (externus). Both branches extend ventrally overlapping each other to insert on the retroarticular process.

2- Cervicomandibularis

Attaches to the posterior end of the retroarticular process, and inserts on muscle fascia dorsally.

3- Constrictor colli

A narrow rounded muscle that ends on the dorsal side of the neck (plate 7.1.1a).

4- Trapezius

Originates from the mid-dorsal line, and inserts on the anterior edge of the scapulocoracoid.

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

Originates from the lateral arms of the interclavicle (plate 71.1a), and inserts on the paroccipital process laterally.

2- Clavicle dorsalis

Absent.

3- Levator scapulocoracoid dorsalis and ventralis

Both originate from the transverse process of the atlas, and insert on the anterior side of the suprascapula (dorsalis), and the dorsal side of the clavicle (ventralis).

4- Ribs to suprascapula muscle slips

The first, second and third cervical rib muscle slips insert on the suprascapula dorsally. The fourth and fifth cervical ribs insert on the suprascapula posteriorly.

Deep muscles

The dissection here concentrated on the ventral side of the neck region and therefore obliquus and rectus capitis, splenius capitis, spinalis capitis and cervicus, spinalis and semispinalis complex, were not explored in detail during dissection.

1- Longissimus muscle

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches dorsally from the longissimus dorsi, and inserts on the posterodorsal edge of the parietal.

c) Longissimus capitis 2

Branches laterally and inserts on the paroccipital process laterally.

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches laterally from the longissimus dorsi, and inserts on the convex ventrolateral tip of the oto-occipital near the basal tubera.

f) Longissimus capitis minor

Branches from longissimus cervicus, and inserts on the ventrolateral margin of the oto-occipital.

g) Longissimus cervicus

See chapter 1.

2- Iliocostalis muscles

a, b) Iliocostalis major and cervicus:

See chapter 1.

3- Longus colli

Originates from the anterior side of the C8 centrum (plate 7.1.1d), and extends anteriorly with slips from C6-7 centra and from the mid-central keel of C5. The single bundle continues anteriorly, taking slips from the tips of the intercentra before forming a tendinous bundle which inserts on the basal tubera.

4- Reduced longus cervicus (second cervical rib to fourth intercentrum tendon)

This small oblique tendon originates from the second cervical rib, and inserts on the lateral crest of the fourth intercentrum (it may correspond to longus cervicus?).

5- First intercentral muscle slip to basioccipital

Ventrally, the first intercentrum muscle runs anteriorly to insert on the central area of the basioccipital.

6- Posterior (2-4) intercentral muscle slips to the oto-occipital

Ventrally, the second and third intercentral muscle slips insert on the oto-occipital deep to the longus colli insertion and first intercentral muscle slip. The fourth intercentral muscle slip inserts on the ventral end (ridge) of the oto-occipital close to the occipital condyle and internal to longissimus capitis 4 insertion (plate 7.1.1c).

Very deep ventral muscles

1- The cervical and trunk vertebrae central tendon

The tendon starts on the posterior side of the fourth intercentrum, and runs posteriorly and medially along the cervical and trunk vertebrae.

(B) Osteology of *Diploglossus crusculus* (anguid with short limbs)

(Plate 7.1.2)

Skull

1- Parietal

The mid-posterior margin is concave and smooth with shallow lateral concavities. The posterolateral processes are long and wide.

2- Squamosal

A long splint/like bone (plate 7.1.2a).

3- Supratemporal

A small bone that extends along the anterior side of the parietal and the lateral margin of the paroccipital process (plate 7.1.2a). It also contacts the squamosal and quadrate.

4- Quadrate

The posterodorsal process is slightly exposed posteriorly.

5- Retroarticular process

A well-developed process with a wide end and internal concavity.

6- Supraoccipital

It possesses a rounded midline ridge.

7- Oto-occipital

The paroccipital process is wide. The ventrolateral tip of the oto-occipital is convex and at the junction with the basioccipital, bears a shallow ridge (where deep intercentral muscle slips insert).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera bear oval epiphysis.

Presacral vertebral column

1- Atlas

The posterior process is short and projects dorsally. The transverse process is pointed posteriorly. Ventrally the intercentrum is keeled.

2- Axis

The postzygapophyses are smooth and horizontal. The transverse processes project strongly (iliocostalis major). Ventrally, the second intercentrum is deep and pointed posteriorly. The third intercentrum is fused to C2, and to

the second intercentrum. Both intercentra possess lateral crests (where the deep slips of longus cervicus insert).

3- C3-8

There are 8 cervical vertebrae, and 7 keeled intercentra (the two axial intercentra are fused) (plate 7.1.2d). The height of the neural spines is constant anteriorly (C3-6), and increases posteriorly (C7-8). They have triangular tips with short dorsal ends. The anterior margins of the spines are curved and smooth, while the posterior margins are straight. The smooth postzygapophyses are either straight (C3-5), or inclined (<90°-C6-8). Ventrally, the centra are smooth (C2-6), or keeled (C7-8) (plate 7.1.2d). The keeled intercentra are deep and long (blade-like), with sharp (narrow) apices. The second, third and fourth intercentra have posterolateral crests (where longus cervicus muscle slips insert). The intercentra are fused to the centrum in front.

4- Anterior trunk vertebrae

The neural spines are long with laterally compressed tips and straight anterior margins.

5- Ribs

The rib ratio is 3+3+2. The distal ends of the cervical ribs are wide (C4-6) anteriorly and narrow (C7-8) posteriorly (plate 7.1.2d), and possess cartilaginous ends. The shafts bear an anterior keel close to their tips.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

This articulates with both scapulocoracoid and suprascapula dorsally.

3- Interclavicle

This is cruciform with inclined lateral arms and long anterior and posterior stems (plate 7.1.2b) (Camp, 1923; McDowell and Bogert, 1954).

4, 5- Scapulocoracoid and suprascapula

Wide scapulocoracoid which bears a wide flat suprascapula (plate 7.1.2c).

Myology of *Diploglossus crusculus*

(Plate 7.1.3)

Superficial muscles

The depressor and cervicomandibularis, trapezius, constrictor colli and latissimus dorsi muscles were not investigated during this dissection, which concentrated on the ventral region of the neck.

Intermediate muscles

The episternocleidomastoid, clavicle dorsalis, levator scapulocoracoid dorsalis and ventralis, were not investigated during the dissection.

1- Ribs to suprascapula rib muscles

The first, second and third cervical rib muscle slips insert on the suprascapula dorsally (the first rib muscle extends towards the longus colli muscle fascia). The fourth and fifth cervical rib muscle slips insert on the suprascapula posteriorly (plate 7.1.2c).

Deep muscles

1-Longissimus capitis 4

Branches ventrally from longissimus dorsi and inserts on the ventrolateral tip of the oto-occipital (convexity).

2- Superficial second intercentral muscle to suprascapula (Cr2-Ssp)

The second intercentrum gives rise to a narrow tendinous sheet that runs from its anterior apex. It extends posteriorly dorsal to longus colli (along C4-5), where it becomes muscular, and inserts on anterior dorsal edge of the suprascapula (Fig., 7.1.1).

3- Superficial posterior intercentral muscle to cervical ribs (Ic[2-5]-Cr[4-5]):

The muscle originates from the second, third (fused), fourth and fifth intercentra (posterior and parallel to the second intercentral muscle to the suprascapula) as a wide flat tendon sheet that extends posteriorly above longus colli (Fig., 7.1.1). It becomes muscular at C5-6 and inserts on the distal ends of the fourth and fifth cervical ribs. Note: both 2 and 3 run ventrally, superficial to longus colli.

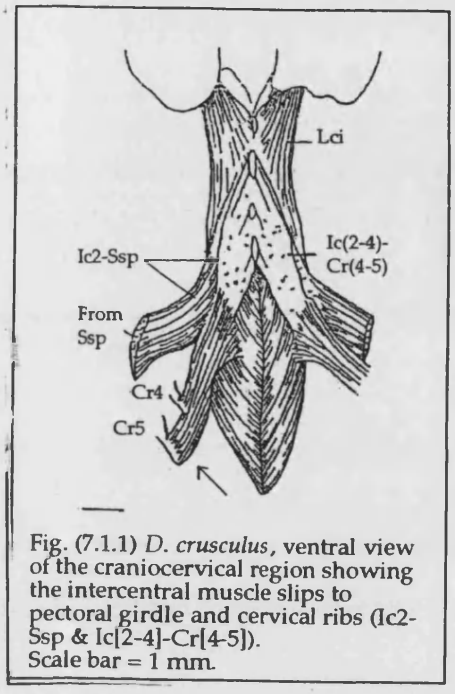


Fig. (7.1.1) *D. crusculus*, ventral view of the craniocervical region showing the intercentral muscle slips to pectoral girdle and cervical ribs (Ic2-Ssp & Ic[2-4]-Cr[4-5]). Scale bar = 1 mm.

4- Longus colli

Originates from the posterior margin of the D2 centrum (plate 7.1.3a), and laterally from D1 centrum, the mid-central keel of C7-8, and the deep intercentral tips of C2-6. The muscle inserts on the basal tubera (muscle bundle).

5- Longus cervicus (superficial, intermediate and deep slips)

Originates from the C7 centrum and C8 rib ligament, and inserts on the second intercentrum. As the muscle extends anteriorly it divides into 3 layers (plate 7.1.3b-d). The superficial layer originates from the mid-central keel of C7 and inserts on the posterior margin of the second intercentrum (lateral crest); the intermediate layer originates from the C4-8 centra and rib ligaments and inserts on the posterior margin of the third intercentrum (lateral crest); the deep layer originates from the C6-8 rib ligaments and inserts on the posterior margin of the fourth intercentrum (lateral crest). After removing the longus cervicus layers, the second, third and fourth intercentra are seen to give origin to a posterior short oblique muscle that

runs to the transverse process of C3-5. These very deep short muscles could be considered as part of longus cervicus or of iliocostalis major.

6- First intercentral muscle slip to basioccipital

Ventrally, this intercentral muscle slip runs anteriorly to insert on the central area of the basioccipital (partially covered by the longus colli).

7- Posterior (2-4) intercentral muscle slips to oto-occipital

Ventrally, the second, third and fourth intercentral muscle slips extend anteriorly to insert on the ventral end of the oto-occipital (ridge) near its junction with the basioccipital, deep to the first intercentral muscle slip.

Comparison of osteological features between short limbed anguids (*Diploglossus*)

An osteological comparison of the neck region between 3 species of genera *Diploglossus* (*D. monotropis, D. shamini* and *D. crusculus*) shows similarities and variation, for details see interspecific section on the discussion.

(C) Osteology of *Ophiodes intermedius* (limbless anguids)

(Plate 7.1.4)

Skull

1- Parietal

The mid-posterodorsal margin is smooth and concave with lateral shallow concavities (where splenius capitis inserts), and long narrow posterolateral processes (where depressor mandibulae externus originates; longissimus capitis 1 insert).

2- Squamosal

An elongated curved splint (where depressor mandibulae internus originates).

3- Supratemporal

A narrow elongated bone that extends along the lateral margin of the parietal and meets the paroccipital process (where depressor mandibulae externus originates). The bone also contacts the squamosal and quadrate.

4- Quadrate

The posterodorsal process is slightly exposed posteriorly (where depressor mandibulae internus originates).

5- Retroarticular process

A well-developed process with a wide posterior end (plate 7.1.4c).

6- Supraoccipital

The midline ridge is rounded (plate 7.1.4a).

7- Oto-occipital

The paroccipital process is short and wide. The ventrolateral end of the oto-occipital near the basal tubera is convex (where longissimus capitis 4 inserts) (plate 7.1.1b), while the border with the basioccipital has a curved ridge (where the intercentral muscle slips insert).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera bear oval epiphyses and the area between the tubera bears a short ridge (no muscle insertion).

Presacral vertebral column

1- Atlas

The posterior process is directed dorsally (plate 7.1.4e) and the transverse process is pointed posteriorly. The intercentrum is keeled.

2- Axis

The postzygapophyses are smooth and inclined. The transverse process is wide and projects posteriorly. Ventrally, the second and third intercentra

are semifused (Hoffstetter and Gasc, 1969) and bear posterolateral crests (where the deep longus cervicus muscle slips insert). The third intercentrum is fused to C2 (plate 7.1.4e).

3- C3-6

There are 6 cervical vertebrae and 6 keeled intercentra (plate 7.1.5e). The height of the neural spines is constant anteriorly (C3-D1), and then increases posteriorly (D2). The ends of the neural spines are triangular with short dorsal tips (plate 7.1.4f). The anterior margins of the spines are curved and smooth, while the posterior margins are smooth and straight (plate 7.1.4f). The postzygapophyses are smooth and inclined (<90°). The width of the centra is either equal to the length (C3-4), or is greater (C5-D2). Ventrally, the centra are smooth between the intercentra (ends on C5), but have midline keels posteriorly (C6-D2). The intercentra are fused to the centrum in front. The second, third and fourth intercentra have posterolateral crests (where longus cervicus muscle slips attach), while the posterior intercentra are smooth.

4- Anterior trunk vertebrae

The neural spines are long with compressed tips. Their anterior margins are straight.

5- Ribs

Rib ratio is 3+2+1 (plate 7.1.5e). The distal ends of all cervical ribs are narrow with cartilaginous ends. The shafts are smooth and flat.

Pectoral girdle

1- Sternum

This is a small cartilaginous plate.

2-Clavicle

This is imperforate and articulates with the weakly-developed scapulocoracoid and suprascapula.

3-Interclavicle

This is cruciform with long narrow lateral arms, and short anterior and posterior processes (plate 7.1.4d) (Camp, 1923).

4, 5- Scapulocoracoid and suprascapula

The scapulocoracoid is short and bears a long narrow suprascapula.

Muscles in *Ophiodes intermedius*

(Plate 7.1.5)

Superficial muscles

1- Depressor mandibulae internus and externus

This originates from the squamosal and quadrate (internus), and from the supratemporal, parietal and muscle fascia of longissimus capitis 1 (externus) (plate 7.1.5c). Both branches extend ventrally overlapping each other to insert on the retroarticular process.

2- Cervicomandibularis

Originates from the muscle fascia of longissimus capitis, and inserts on the external process of the articular.

3- Constrictor colli

A flat, wide thin muscle that runs around the neck. It inserts on the muscle fascia of longissimus capitis 1 (plate 7.1.5a).

4- Trapezius

It originates dorsally from the muscle fascia of the splenius capitis, and inserts on the short elongated scapulocoracoid.

5- Latissimus dorsi

Originates from the clavicle and scapulocoracoid, and inserts on the muscle fascia of the splenius capitis (plate 7.1.5a).

Intermediate muscles

1- Episternocleidomastoid

It originates from the clavicle, and inserts on the ventrolateral side of the paroccipital process (plate 7.1.5b).

2- Clavicle dorsalis

It originates from the muscle fascia of longissimus capitis 1 (plate 7.1.5b), and inserts on the anterolateral side of the clavicle (dorsal to the episternocleidomastoid origin).

3- Levator scapulocoracoid dorsalis and ventralis

They originate from the transverse process of the atlas, and insert on the anterior margin of the narrow suprascapula.

4- Ribs to suprascapula muscle slips

The first, second and third cervical rib muscle slips insert on the suprascapula dorsally. The first trunk rib (fourth rib) muscle slip inserts on the suprascapula and scapulocoracoid posteriorly.

Deep muscles

1- Rectus and obliquus capitis

Both muscles originate from the anterior cervical vertebrae, and extend anteriorly to insert on the dorsal side of the supraoccipital (rectus), and paroccipital process (obliquus).

2- Splenius capitis

It originates above the cervical neural spines and laterally from muscle fascia and extends anteriorly as one trunk to insert on the posterodorsal midline of the parietal (shallow concavity).

3- Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches dorsally from the longissimus dorsi, and inserts on the dorsolateral side of the parietal.

c) Longissimus capitis 2

Branches laterally from the longissimus dorsi, and inserts on the lateral and ventral surfaces of the paroccipital process.

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches ventrally from the longissimus dorsi, and inserts on the ventrolateral end of the oto-occipital (convexity).

f) Longissimus capitis minor

Branches ventrolaterally from the longissimus cervicus, and inserts on the ventrolateral margin of the oto-occipital.

g) Longissimus cervicus

See chapter 1.

4-Iliocostalis muscles

a) Iliocostalis major

See chapter 1.

b) Iliocostalis cervicus

Absent

Ventral deep muscles

1- Superficial first intercentrum to suprascapula tendinous muscle (Ic1-Ssp):

The first intercentrum gives attachment to a narrow tendon sheet that starts on its posterior apex. This extends posteriorly above longus colli (along C3-4), where it becomes muscular. It finally inserts on the anterodorsal edge of the suprascapula (plate 7.1.5d).

2- Superficial posterior intercentral tendinous muscle to third cervical rib (Ic[2-5]-Cr3):

The second, third (semifused), fourth and fifth intercentra give attachment to a wide flat tendinous sheet that extends posteriorly towards the end of longus colli (as a narrow bundle). The sheet becomes muscular above longus colli (C4), and inserts on the distal end of C6 rib (last cervical rib) (plate 7.1.5d).

3-Longus colli

It originates from the anterior edge of the D3 centrum (plate 7.1.5e), and extends anteriorly taking slips from the mid-central keel of C6-D2 and the six intercentra of C1-5. The muscle inserts on the basal tubera (as muscle fibers).

4- Longus cervicus

It originates from the anterior margin of the C6 centrum and rib ligament, and extends anteriorly to insert on the posterolateral crest of the second, third and fourth intercentra (plate 7.1.5e).

5- First intercentral muscle slip to basioccipital

Ventrally, the first intercentral muscle extends anteriorly to insert on the basioccipital deeper to the longus colli insertion.

6- Posterior (2-5) intercentral muscle slips to oto-occipital

The second to fifth intercentral muscle slips extend anteriorly to insert on the ventral end of the oto-occipital close to the occipital condyle (curved

ridge) (plate 7.1.5d). Ventrally, the posterior muscle slips insert deep to the first intercentrum to basioccipital muscle.

Very deep muscles

1- The cervical and trunk vertebrae central tendon

The tendon starts on the posterior side of the sixth intercentrum and runs posteriorly and medially along the cervical and trunk vertebrae.

Comparison of osteological features between anguids

(Ophiodes and Anguis)

A comparison of the neck anatomy between two genera *Ophiodes* (*O. intermedius* and *O. striatus* [skeleton]) and *Anguis* (*A. fragilis*) shows similarities and variation as follows.

1) Similarities between *Ophiodes* and *Anguis*:

Excluding general similarities found in other lizards:

- The sternum is reduced.
- The episternocleidomastoid originates from the clavicle.
- The first intercentral muscle slip inserts completely under longus colli insertion.
- The first cervical rib muscle slip to suprascapula is present.

2) Variation between *Ophiodes* and *Anguis*:

- In *Ophiodes*, there is a short ridge between the basal tubera (for the first intercentral muscle), while in *Anguis*, there is a long thick keel for both the first intercentral muscle and the clavicle to basioccipital muscle insertion (*Anguis*).
- In *Ophiodes*, the second intercentrum has lateral crests (where longus cervicus inserts), while in *Anguis* it is smooth (where longus cervicus is absent).

- There are 5 keeled intercentra (*Anguis*) or 6 (*Ophiodes*). In *Ophiodes*, they are deep with sharp apices, while in *Anguis* they are shallower. The intercentra are smooth posteriorly (*Anguis*) or have lateral crests (*Ophiodes*). Also in *Ophiodes*, the three centra after the last keeled intercentra have a midline keel, which sometimes extends towards the anterior dorsal centra, while the centra in *Anguis* are smooth.

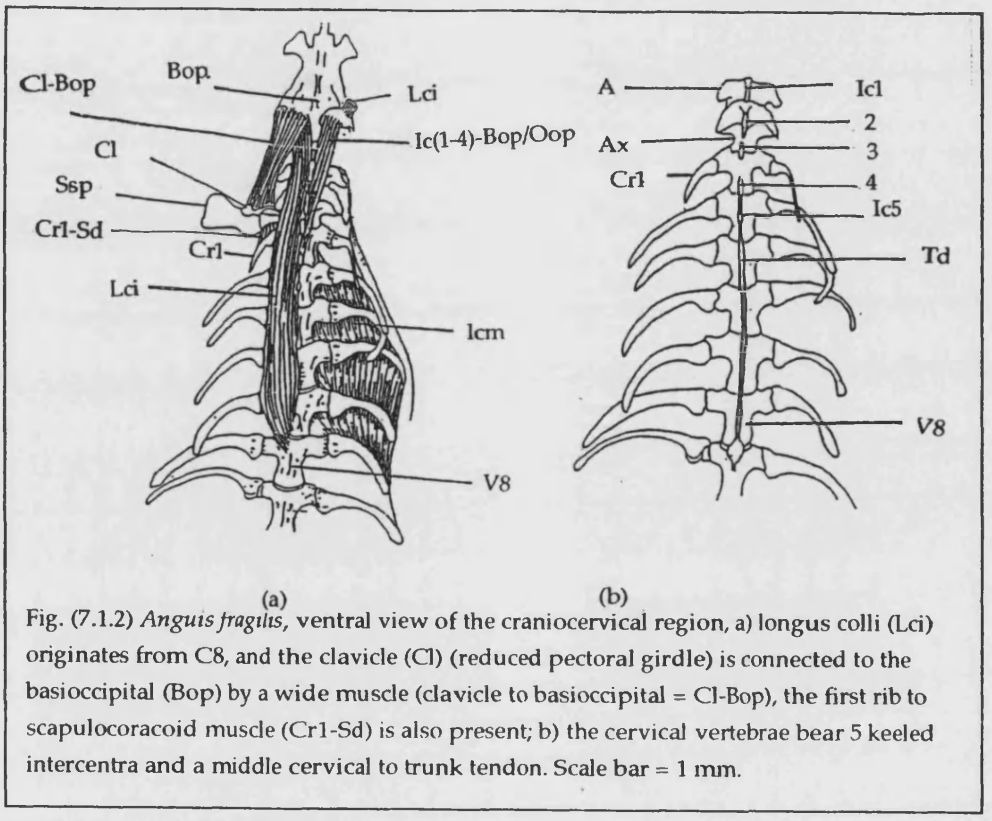


Fig. (7.1.2) *Anguis fragilis*, ventral view of the craniocervical region, a) longus colli (Lci) originates from C8, and the clavicle (Cl) (reduced pectoral girdle) is connected to the basioccipital (Bop) by a wide muscle (clavicle to basioccipital = Cl-Bop), the first rib to scapulocoracoid muscle (Cr1-Sd) is also present; b) the cervical vertebrae bear 5 keeled intercentra and a middle cervical to trunk tendon. Scale bar = 1 mm.

- In *Ophiodes* the trunk ribs attach to the poorly developed sternum, but in *Anguis* the ribs are free.
- In *Ophiodes*, the clavicle is long and curved, while in *Anguis*, it is short and reduced.
- The interclavicle is present in *Ophiodes*, while in *Anguis* it is absent, although Parker (1868) figured the interclavicle in *Anguis*.

- In *Anguis*, scapulocoracoid and suprascapula are situated anteriorly around the level of C2, but in *Ophiodes* they are situated posteriorly around the level of C7.
- In *Ophiodes*, the latissimus dorsi is present, but I did not investigate the muscle in *Anguis*.
- In *Ophiodes*, the longus colli starts origin from 8^{9h} centrum (anterior edge), while in *Anguis*, it starts from 8th and 9th centrum (anterior edge).
- There are 3 posterior intercentral muscle slips to the skull in *Ophiodes*, and 4 slips in *Anguis*.
- In *Ophiodes*, the longus cervicus is present, but not investigated in *Anguis*.
- In *Ophiodes*, there are 1st, 2nd, 3rd and 4th rib to suprascapula muscle slips, but in *Anguis* there is one rib to scapulacoracoid muscle slip.
- Intercentral tendinous muscles to suprascapula and ribs are present in *Ophiodes*, but not investigated in *Anguis*.

Note: the clavicle to basioccipital tendinous muscle in *Anguis fragilis* might be equivalent to clavicle dorsalis in *Ophiodes intermedius*.

Comparison of osteological and muscular features within Anguidae

A comparison of the neck anatomy between anguids with well-developed limbed (*Elgaria*), short limbed anguids (*Diploglossus*) and limbless anguids (*Ophiodes*) shows similarities and variation. Some muscles were not investigated or observed because of poorly preserved specimens.

1) Similarities between *Elgaria, Diploglossus* and *Ophiodes*:

Excluding general similarities found in other lizards.

- The ventrolateral end of the oto-occipital is convex (where longissimus capitis 4 inserts).

- The ventral end of the oto-occipital close to the occipital condyle has a curved ridge (where intercentral muscles to skull insert).
- Centra behind the last intercentra are keeled.
- Interclavicle is cruciform.
- Depressor mandibulae internus originates from the parietal, supratemporal and muscle fascia. (This feature was not investigated in *Diploglossus*).
- Trapezius inserts on the scapulocoracoid (*Diploglossus* not investigated).
- Episternocleidomastoid inserts on the paroccipital process (*Diploglossus* not investigated).
- Longus colli originates from the centra.
- Ventrally, posterior intercentral muscle slips insert on the oto-occipital deep to the first intercentral muscle slip.
- Cervical and trunk central tendon is present.

2) Variation between *Elgaria, Diploglossus* and *Ophiodes*:

- The number of the cervical vertebrae is 8 (limbed *Elgaria* and *Diploglossus*) or 6 (limbless *Ophiodes*).
- The degree of depth of the intercentra is shallow (*Elgaria*), moderate (*Diploglossus*), or deep (*Ophiodes*).
- In *Diploglossus* and *Ophiodes*, lateral crests are present on the 2nd, 3rd and 4th intercentra, while in *Elgaria* on the 4th intercentrum only (reduced longus cervicus).
- In *Diploglossus* and *Ophiodes*, basal crests are absent, but they present in *Elgaria*.

- In *Elgaria* and *Diploglossus* (limbed), the cervical centra behind the intercentra are keeled, while in *Ophiodes* (limbless), the anterior dorsal centra are keeled as well.
- The rib ratio = 3+3+2 (limbed *Elgaria* and *Diploglossus*), or 3+2+1 (limbless *Ophiodes*).
- The sternum, suprascapula and scapulocoracoid are well - developed in *Elgaria* and *Diploglossus*, and reduced in *Ophiodes*.
- The episternocleidomastoid originates from the interclavicle (*Elgaria*, not observed in *Diploglossus*), or clavicle (*Ophiodes*).
- The clavicle dorsalis is absent in *Elgaria* (not observed in *Diploglossus*), and present in *Ophiodes*.
- Ribs to suprascapula muscle slips originate from cervical vertebrae (*Elgaria* and *Diploglossus*), or from cervical and dorsal vertebrae (*Ophiodes*).
- The longus colli originates from C8 (*Elgaria*), D2 (*Diploglossus*) or D3 (*Ophiodes*).
- The longus cervicus is well-developed in *Diploglossus* and *Ophiodes*, and reduced (one short tendon) in *Elgaria*.
- Longus cervicus originates from 2nd cervical rib of C5 (*Elgaria*), C7 and C8 rib ligament (*Diploglossus*) or C6 centrum and rib ligament (*Ophiodes*).
- Intercentra to suprascapula tendinous muscles are present in *Diploglossus* and *Ophiodes*, and absent in *Elgaria*.
- The first intercentral muscle slip inserts on the basioccipital partially deep to longus colli insertion (*Elgaria* and *Diploglossus*), or completely deep to longus colli insertion (*Ophiodes*).

- There are 3 posterior intercentral muscle slips to skull (*Elgaria* and *Diploglossus*), or 4 slips (*Ophiodes*).

Anatomy of the neck region in Xenosauridae

I dissected *Shinisaurus crocodilurus* in detail.

Previous works:

Camp, 1923; Barrows and Smith, 1947; McDowell and Bogert, 1954; Jollie, 1960; Hoffstetter and Gasc, 1969; Costelli and Hecht, 1971; Rieppel, 1980; Gao and Norell, 1998.

Osteology of *Shinisaurus crocodilurus*

(Plate 7.2.1)

Skull

1- Parietal

The mid-posterodorsal margin is smooth with shallow concavities Plate (7.2.1c) (where splenius capitis inserts). The posterolateral processes are long and narrow (where longissimus capitus 1 inserts).

2- Squamosal

A long splint of bone with a strong process that arches ventrally to contact the quadrate (plate 7.2.1c) (Barrow and Smith, 1947; McDowell and Bogert, 1954; Rieppel, 1980a) (where depressor mandibulae internus originates).

3- Supratemporal

This elongated narrow bone (the tabular of McDowell and Bogert, 1954) extends along the anterolateral edge of the parietal and the paroccipital lateral margin (where depressor mandibulae externus originates). It also contacts the squamosal, oto-occipital and quadrate (Barrow and Smith, 1947).

4- Quadrate

The posterodorsal process is strongly curved (where depressor mandibulae internus originates).

5- Retroarticular process

This well-developed process has a wide posterior end.

6- Supraoccipital

There is a rounded midline ridge (Barrow and Smith, 1947).

7- Oto-occipital

The paroccipital process is wide (Barrow and Smith, 1947), and the ventrolateral margin has a long narrow crista tuberalis.

8- Paroccipital and quadrate epiphyses

Absent, but several authors like Camp (1923 – "paroccipital"), Barrows and Smith (1947), Mc Dowell and Bogert (1954), and Jollie (1960) have described a small ossified intercalary between the supratemporal, paroccipital process and the top of the quadrate.

9- Basioccipital

The basal tubera have a wide elongated epiphysis (the dorsal end where the longissimus capitis 4 inserts), but Barrow and Smith (1947) reported two small basioccipital tubera.

Presacral vertebral column

1- Atlas

The posterior process is short and the transverse process is deep. The first intercentrum is keeled.

2- Axis

The postzygapophyses are horizontal and bear tubercles. The transverse processes project weakly. Ventrally, the second and third intercentra are very close (centrum lacks median keel). The second intercentrum is smooth and shallow, while the third intercentrum is wide, deep and has one pair of

lateral crests (where the tendon to the third transverse process originates) (plate 7.2.2d). The third intercentrum is fused to C2 (i.e. centrum in front). In *Carusia* (primitive extinct Anguimorpha) the third intercentrum is free from the axis (Gao and Norell, 1998).

3- C3-8

There are 8 cervical vertebrae (McDowell and Bogert, 1954; Hoffstetter and Gasc, 1969), and 5 keeled intercentra (plate 7.2.2d). The height of the neural spines is constant (C2-6), and then increases (C7-8). The neural spine tips are triangular with short dorsal ends. The anterior margins of the spines are smooth and curved, while the posterior margins are straight. The postzygapophyses are smooth. Ventrally, the centra are keeled (C3-4), then rounded (C5-6), and then become flat (C7-8). The intercentra are shallow with a long apex. They possess lateral crests (where tendons to the transverse processes originate), and are fused to the centra in front. The position of the intercentra and the presence of the crests are the same *Xenosaurus grandis* (Barrows and Smith, 1947).

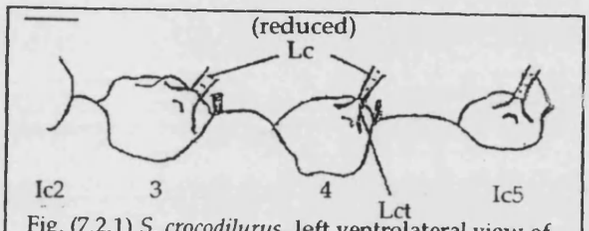


Fig. (7.2.1) *S. crocodilurus*, left ventrolateral view of the cervical vertebrae showing 3rd –5th intercentra with lateral crests (Lct) for reduced longus cervicus (Lc). They are fused to centrum in front. Scale bar = 1 mm.

4- Anterior trunk vertebrae

The neural spines are long and wide with compressed dorsal tips. The anterior margins are smooth and curved, while the posterior margins are curved.

5- Ribs

Rib ratio 3+3+2 (plate 7.2.2a) (Costelli and Hecht, 1971), although there are 3 cervical ribs in *Xenosaurus grandis* (Barrows and Smith, 1947). Hoffstetter and Gasc (1969) also recorded the first cervical rib on the third cervical

vertebra. The distal end of the first cervical vertebrae is wide, while the posterior cervical ribs are pointed and bear cartilaginous ends. The shafts are smooth and flat, and are connected to the keeled intercentra by ligaments.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

It extends across the anterior margin of the scapulocoracoid and ends along the suprascapula dorsally (as in *Xenosaurus grandis* – Barrows and Smith, 1947).

3- Interclavicle

This cruciform bone has long narrow lateral arms (plate 7.2.1d) (where episterno-cleidomastoid originates) and both anterior and posterior stems (the lateral arms are inclined to the horizontal) (McDowell and Bogert, 1954; Costelli and Hecht, 1971). Barrows and Smith (1947) described an anchor-shaped interclavicle in *Xenosaurus grandis*.

4, 5- Scapulocoracoid and suprascapula

The scapulocoracoid is wide (where trapezius inserts), and bears a wide flat suprascapula.

Muscles in *Shinisaurus crocodilurus*

(Plate 7.2.1 – 7.2.2)

Superficial muscles

1-Depressor mandibulae (internus and externus)

Originates from the quadrate (dorsal posterolateral margin), and squamosal (lower posterolateral part) as the internus branch, and from the supratemporal (along the posterolateral margin) and muscle fascia as the

externus branch (plate 7.2.1b). Both branches extend ventrally (overlapping each other) to insert on the retroarticular process.

2- Cervicomandibularis

Originates broadly from the muscle fascia of splenius capitis, and inserts on the articular process.

3- Constrictor colli

A thin flat muscle that runs around the neck region and from an origin on longissimus capitis 1.

4- Trapezius

Originates from the mid-dorsal line, and inserts on the anterolateral side of the scapulocoracoid (plate 7.2.1a).

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

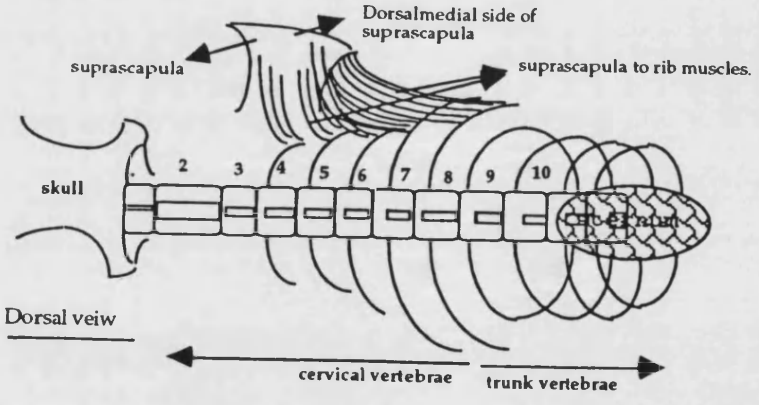


Diagram (7.2.1) left dorsal view of the craniocervical region with cervical rib to suprascapula muscle slips in *Shinisaurus crocodilurus*.

1-Episternocleidomastoid

Originates from the lateral arm of the interclavicle (plate 7.2.1d) and inserts on the lateral edge of the paroccipital process (marked by longitudinal striae).

2-Clavicle dorsalis

Absent.

3- Levator scapulocoracoid dorsalis and ventralis

Both originate from the atlas transverse process, and insert posteriorly on the suprascapula (dorsalis), and the clavicle (ventralis).

4- Ribs to suprascapula muscle slips

The first and second rib muscle slips insert on the anterodorsal side of the suprascapula. The third rib muscle slip inserts on the posterodorsal side of the suprascapula, the fourth and fifth rib muscle slips insert further posteriorly.

Deep muscles

1-Obliquus capitis

Originates from the neural spines of C2-3, and extends anteriorly to insert on the dorsal margin of the paroccipital process close to its suture with the supraoccipital.

2-Rectus capitis

Originates from C1-2 neural spines, and inserts on the dorsal side of the supraoccipital.

3- Splenius capitis

Originates above C7-D1 neural spines and muscle fascia of longissimus capitis 1 laterally. It extends anteriorly and branches to insert on the muscle fascia of longissimus capitis 1 and the posterodorsal side (shallow concavities) of the parietal (plate 7.2.1c).

4-Spinalis/semispinalis muscles

a) Spinalis capitis

Originates deep to splenius capitis from C7-8 neural spines, which are long and narrow. It branches laterally along C5-6 to insert on the muscle fascia of

splenius capitis. The muscle ends on the posterodorsal mid-point of the parietal under the splenius capitis insertion.

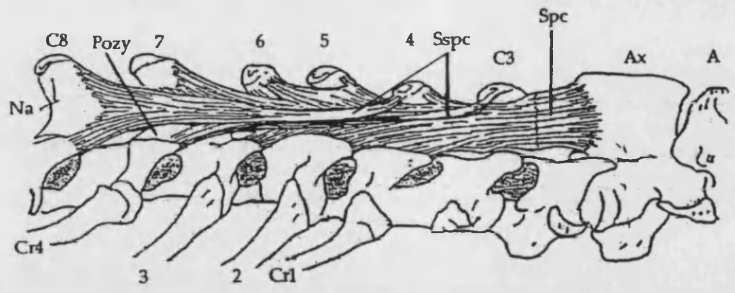


Fig. (7.2.2) *S. crocodilurus*, right lateral view of the cervical vertebrae showing spinalis cervicus (Spc) from neural arches (Na) and postzygapophyses (Pozy) of C3-7, and inserting on the neural arch and postzygapophyses (Pozy) of the axis (Ax). The C8 neural arch and postzygapophyses muscle inserts anteriorly on C3 & C4 neural spines. This represent the first anterior insertion of spinalis/semispinalis complex = spinalis/semispinalis cervicus (Sp/Sspc). Scale bar = 1 mm.

b) Spinalis cervicus

It is visible after removing spinalis capitis and originates from the anterior margins and postzygapophyses of C3-6. It inserts on the posterior edge of the axis neural arch and postzygapophyses tubercles (muscle fibres).

c) Spinalis semispinalis complex

See chapter 1.

5-Longissimus muscles

a) Longissimus dorsi

See chapter 1.

b) Longissimus capitis 1

Branches dorsally to insert on the posterodorsal edge of the parietal.

c) Longissimus capitis 2

Branches laterally to insert on the lateral and ventral sides of the paroccipital process.

d) Longissimus capitis 3

Absent.

e) Longissimus capitis 4

Branches ventrally from the longissimus dorsi along the lateral side of the axis, and extends ventrally to insert on the dorsal extension of the basal tubera.

f) Longissimus capitis minor

Branches from the lateral side of the longissimus cervicus, and extends ventrally to insert on the ventrolateral margin of the oto-occipital (crista tuberalis).

g) Longissimus cervicus

See chapter 1.

8- Iliocostalis muscles

a) Iliocostalis major

See chapter 1.

b) Iliocostalis cervicus

See chapter 1.

9- Longus colli

Originates from the anterior margin of C8 (plate 7.2.2a), and extends anteriorly in three sections, the long section extends laterally from C5-7 and along the centra to attach along C1 under the middle section; the middle section has slips from the 3rd -5th intercentral apices; the short section has slips from the 1st –2nd intercentral apices. The muscle then inserts on the elongated basal tubera (as muscle fibres).

10- Reduced longus cervicus (third transverse process, first and second cervical ribs to third , fourth and fifth intercentral tendons (Cr[1-2]-Ic[3-5]):

The tendon slips start from the third transverse process and first and second cervical ribs to insert anteriorly on the lateral crests of the third, fourth and

fifth intercentra (plate 7.2.2d). These tendons could represent a reduced longus cervicus.

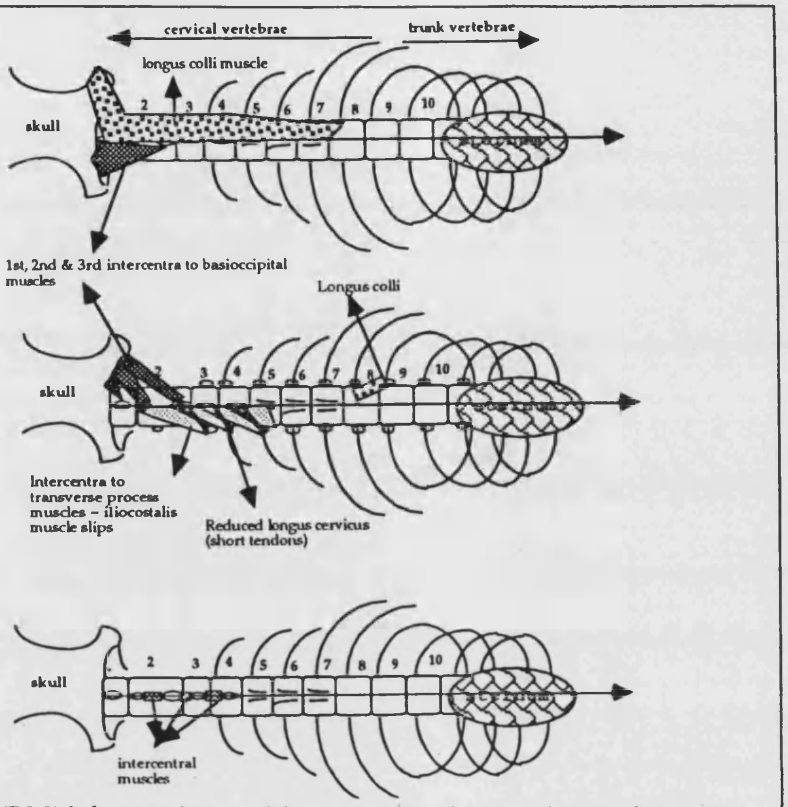


Diagram (7.2.2) left ventral view of the craniocervical region showing longus colli, intercentral muscle slips to skull, reduced longus cervicus (tendons between intercentra 3-5 and transverse processes) in *Shinisaurus crocodilurus*.

11- First intercentrum to basioccipital

Ventrally, the first intercentral muscle slips inserts on the basioccipital deep to the longus colli insertion.

12- Posterior (second and third) intercentral muscle slips to basioccipital

Ventrally, they arise from the second and third intercentra, and insert anteriorly on the basioccipital (rough area with pits and small fossa) deep to the first keeled intercentral muscle insertion (plate 7.2.2c).

Anatomy of the neck region in Helodermatidae

I dissected *Heloderma horridum* in detail.

Previous works:

Boulenger, 1891; McDowell and Bogert, 1954; Hoffstetter and Gasc, 1967; Lécuru, 1968; Pregill et al., 1986; Estes et al., 1988; Herrel and De Vree, 1999.

Osteology in *Heloderma horridum*

(Plate 7.3.1)

Skull

1- Parietal

The mid-posterodorsal margin is smooth with shallow concavities. The posterolateral processes are long and narrow.

2- Squamosal

A short curved splint-like bone that does not meet the paroccipital process (plate 7.3.1a). It is shorter than the supratemporal (McDowell and Bogert, 1954).

3- Supratemporal

This narrow elongated bone extends along the lateral edge of the parietal and the paroccipital lateral margin. It also contacts the squamosal (McDowell and Bogert, 1954).

4- Quadrate

The posterodorsal process is strongly curved.

5- Retroarticular process

This well-developed process has a wide posterior end.

6- Supraoccipital

There is a shallow midline keel.

7- Oto-occipital

The paroccipital process is narrow. The ventrolateral tip of the oto-occipital near the basal tubera is convex. The ventral end of the oto-occipital close to the suture with the basioccipital has a shallow ridge (where posterior intercentral muscle slips insert).

8- Paroccipital and quadrate epiphyses

Absent.

9- Basioccipital

The basal tubera have rounded epiphyses.

Presacral vertebral column

1- Atlas

The mid-dorsal line is narrow and possesses a dorsal crest (where rectus capitis originates). The posterior process is long and pointed dorsally. The transverse process is pointed posteriorly. The first intercentrum is shallow (Boulenger, 1891).

2- Axis

The postzygapophysis is horizontal and bears a small tubercle. The transverse process is wide and projects posteriorly. Ventrally, the centrum is smooth and the second intercentrum (= anterior intercentrum) is flat. The third intercentrum is keeled, but is shallow and fused to C2 (i.e. in front) (plate 7.3.1d).

3- C3-8

There are 8 cervical vertebrae (Boulenger, 1891 – *Heloderma suspectum;* McDowell and Bogert, 1954), and 4 weakly - developed intercentra (3 keeled + 1 flat) (plate 7.3.2c, d) (Hoffstetter and Gasc, 1967; Pregill et al., 1986; Estes et al., 1988). The tallest neural spine is C3, then they become constant along C4-7, after which spine height increases on C8. The tips of the neural spines are triangular (C2-5), and compressed (C6-8), and the dorsal ends are short and narrow. The anterior and posterior margins of the spines are straight. In dorsal view, the length of neural arches is equal to the width. The postzygapophyses are inclined and smooth. Ventrally, the centra are smooth. C3 has a shallow rounded fourth keeled intercentrum, which

is fused to C3. The rest of the cervical centra lack intercentra and become smooth after C5 (plate 7.3.2c).

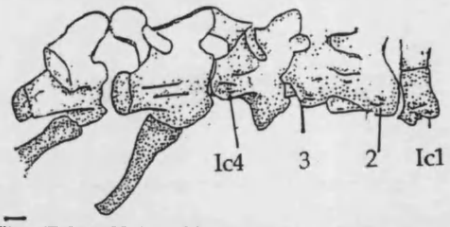


Fig. (7.3.1) *H. horridum*, right ventral view of the anterior cervical vertebrae showing 4 weakly keeled i anterior intercentra (Ic1-4). Scale bar = 1 mm.

4- The anterior trunk vertebrae

The neural spines are long with compressed tips. Their anterior and posterior margins are straight. The neural arches are wider than they are long.

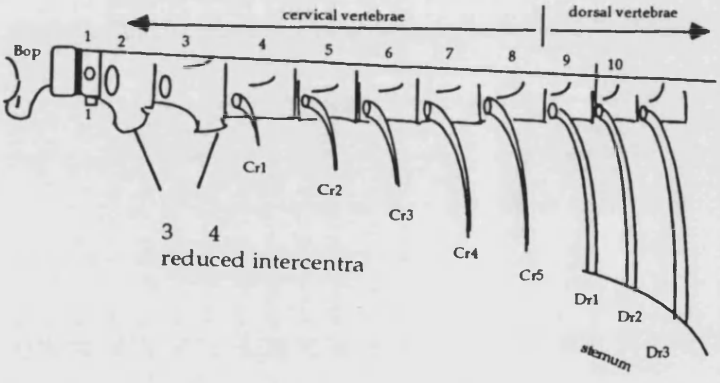


Diagram (7.3.1) Lateral view of the cervical vertebrae in *Heloderma horridum*.

5- Ribs

The rib ratio=3+3+2, although Boulenger (1891) reported that the first cervical rib articulates on the third cervical vertebra in *H. horridum* and on the fourth cervical vertebra in *H. suspectum*. The distal ends of the cervical ribs are pointed and have cartilaginous ends. The shafts of the second, third and fourth cervical ribs bear a posterior crest (iliocostalis muscle slips attachment). The ribs are connected to the transverse process by a short ligament.

3- First intercentrum to basioccipital muscle

Ventrally, the first intercentrum muscle extends anteriorly to insert on the basioccipital completely deeper to longus colli (plate 7.3.2b).

4- Posterior third intercentral muscle slip to basioccipital and oto-occipital

Ventrally, the third intercentral muscle slip inserts on the basioccipital and oto-occipital superficial to the first intercentral muscle slip (plate 7.3.2b). The second flat intercentral muscle is absent.

Anatomy of the neck region in Varanidae

I dissected *Varanus griseus*, *Varanus doreanus* and *Varanus jobiensis*. A skeleton of *Varanus gilleni* and *Varanus prasinus* were also examined. For my detail anatomical description I selected *V. griseus*.

Previous work:

McDowell and Bogert, 1954; Russell, 1967; Bellairs, 1969; Hoffstetter and Gasc, 1969; Rieppel, 1980; Estes et al., 1988; Lee, 1997.

Osteology in *Varanus griseus*

(Plate 7.4.1)

Skull

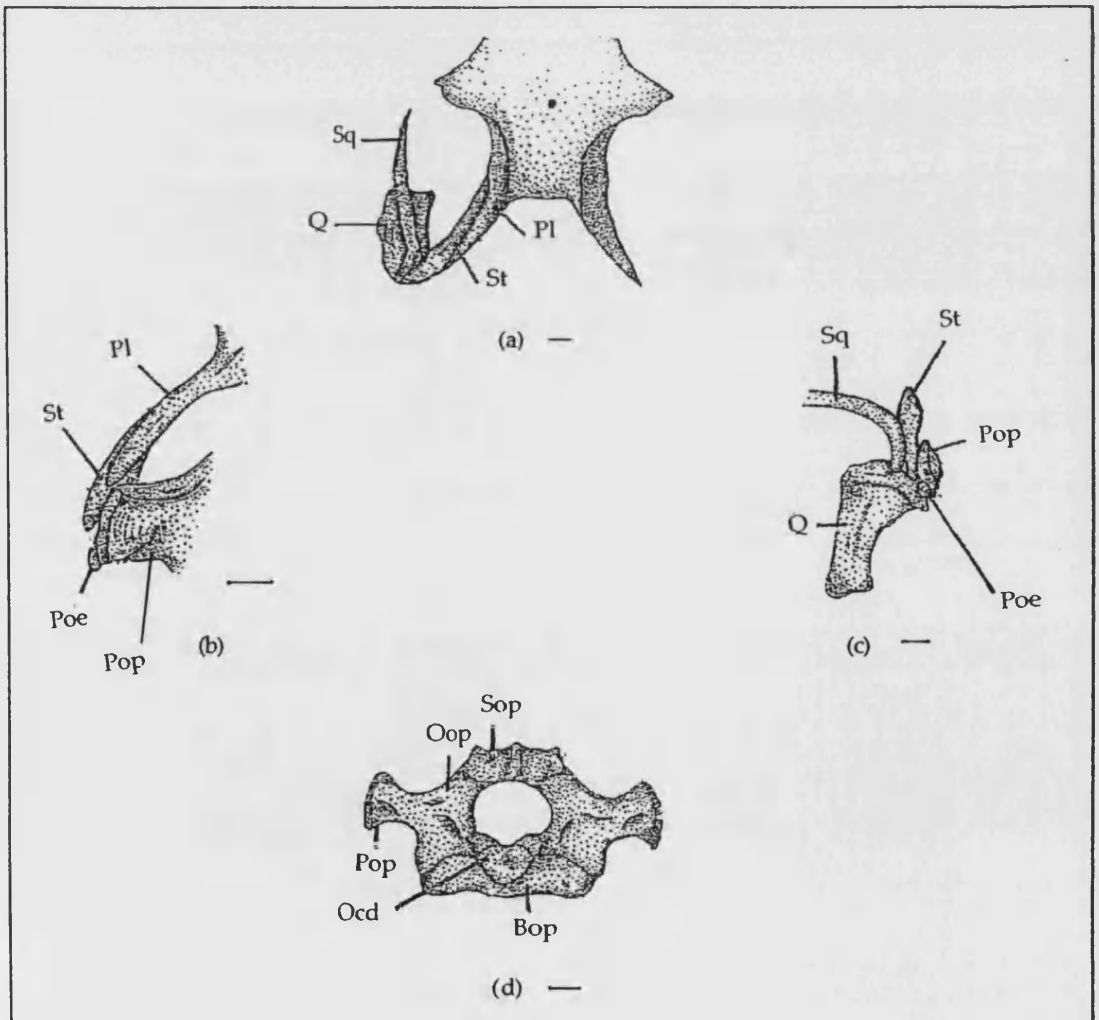


Fig. (7.4.1) *V. griseus*. a) Dorsal view of the skull showing the skull roof; b) Occipital view of skull showing lateral skull components; c) lateral view of the skull showing the quadrate (Q); d) Occipital view of the braincase showing supraoccipital (Sop), oto-occipital (Oop), basioccipital (Bop), supratemporal (St), paroccipital epiphyses (Poe). Scale bar = 1 mm.

1-Parietal

The mid-posterodorsal margin is smooth with shallow concavities (where splenius capitis inserts). The posterolateral processes are long and narrow (where depressor mandibulae externus originates; longissimus capitis 1 inserts).

2-Squamosal

This is a long splint-shaped bone (where depressor mandibulae internus originates) that does not meet the paroccipital process (plate 7.4.1d) (McDowell and Bogert, 1954).

3- Supratemporal

This is long wide bone that extends along the parietal posterolateral processes and the paroccipital lateral margin (McDowell and Bogert, 1954) (where depressor mandibulae internus and externus originate). The bone also contacts the squamosal and quadrate.

4- Quadrate

The posterodorsal process is slightly exposed (plate 7.4.1d) (where depressor mandibulae internus originates).

5- Retroarticular process

It is well-developed (Fig., 7.4.2).

Fig. (7.4.2) *V. griseus*, left lateral view of the lower jaw showing the well-developed retroarticular process (Rp) in *Varanus*. Scale bar = 1 mm.

6- Supraoccipital

This has a rounded midline ridge.

7- Oto-occipital

The paroccipital process is long and narrow (where constrictor colli attaches; longissimus capitis 2 and minor insert). The ventrolateral margin is convex with a long narrow crista tuberalis (plate 7.4.2d) (where longissimus capitis 4 inserts and posterior hypapophyses muscle slips attach).

8- Paroccipital epiphyses

The paroccipital process has an ossified oval epiphysis (plate 7.4.2c) (where episternocleidomastoid attaches).

9- Basioccipital

The basal tubera have elongated narrow epiphyses (where the curved tendons of the longus colli insert).

Presacral vertebral column

1- Atlas

The posterior process is short and narrow (plate 7.4.1a). The first intercentrum is keeled.

2- Axis

The postzygapophysis has a posterior process and the transverse process projects weakly. The second intercentrum has one pair of crests (where longus cervicus tendon ends), while the third intercentrum is fused to the C2 centrum (plate 7.4.1b).

3- C3-9

There are 9 cervical vertebrae (Hoffstetter and Gasc, 1967; Russell, 1967), and 10 keeled hypapophyses (plate 7.4.5b). The heights of the cervical neural spines are constant, and they have long dorsal ends with oval tips. The anterior and posterior margins of the neural spines are straight, and oriented vertically in relation to the neural arch and centrum. The neural arches are longer than they are wide, and the cervical neural arches are longer than the trunk neural arches (Hoffstetter and Gasc, 1969). The postzygapophyses are horizontal, keeled (dorsally) and have posterior processes (where spinalis and semispinalis cervicus attach). Ventrally, the centra are smooth, the hypapophyses are sutured and they attach to the rear of the preceding centrum (plate 7.4.1b) (Hoffstetter and Gasc, 1969). The

apices of the cervical hypapophyses bear lateral distal epiphyses (7.4.1b) (where the deep lateral longus cervicus tendons and hypapophyses to pectoral girdle muscles attach) and large central distal epiphysis (where the longus cervicus middle tendon and longus colli attach). The posterior hypapophyses lack central epiphyses.

4- Anterior trunk vertebrae

The centra are longer than they are wide and the neural spines are long and their dorsal ends are compressed. Their anterior and posterior margins are straight.

5- Ribs

The rib ratio is 5+2+2 (Hoffstetter and Gasc, 1969). The distal end of the first rib is wide, while the posterior cervical ribs are pointed (Fig., 7.4.3). The shafts of the posterior cervical ribs possess posterior crests (iliocostalis muscle slips), and ligaments connect the ribs to the transverse process.

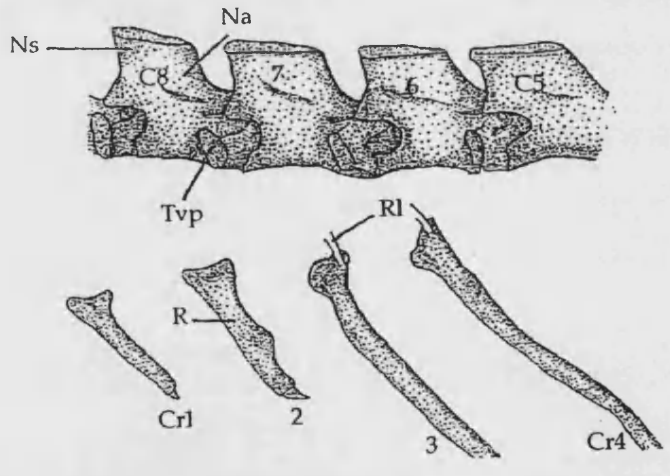


Fig. (7.4.3) *V. griseus*, right lateral view of the posterior cervical vertebrae. The cervical ribs bear rib ligaments (Rl) to the centra. Neural spine (Ns), neural arch (Na), transverse process (Tvp). Scale bar = 1 mm.

Pectoral girdle

1- Sternum

Well-developed.

2- Clavicle

This curved long bone (where episternocleidomastoid originates) articulates with both the scapulocoracoid and suprascapula (Fig., 7.4.4b) (Bellairs, 1969).

3- Interclavicle

This is a T-shaped bone with long lateral arms (Fig., 7.4.4a) (Lee, 1997) and a long posterior stem. This anchor-shaped interclavicle was also observed in most varanids, but Estes et al. (1988) recorded a typical cruciform interclavicle for the group.

4, 5- Scapulocoracoid and suprascapula

The scapulocoracoid is wide (where trapezius inserts) and bears a board flat suprascapula.

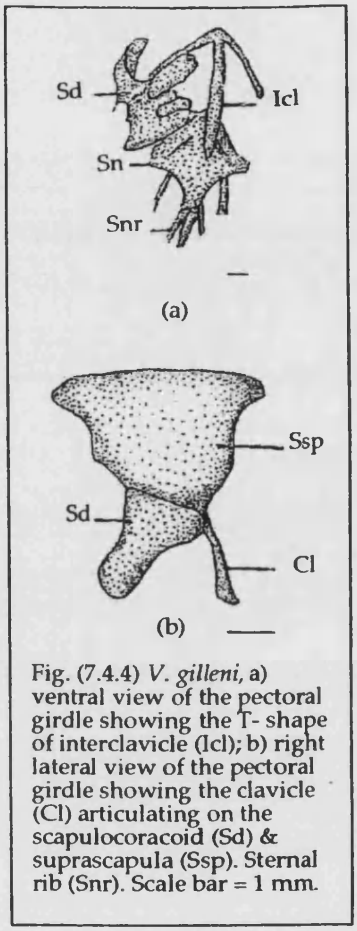


Fig. (7.4.4) *V. gilleni*, a) ventral view of the pectoral girdle showing the T- shape of interclavicle (Icl); b) right lateral view of the pectoral girdle showing the clavicle (Cl) articulating on the scapulocoracoid (Sd) & suprascapula (Ssp). Sternal rib (Snr). Scale bar = 1 mm.

Muscle in *Varanus griseus*

(Plate 7.4.1 - 7.4.2 – 7.4.3 – 7.4.4 – 7.4.5)

Superficial muscles

1- Depressor mandibulae (internus and externus)

It originates from the dorsolateral edge of the quadrate near the ventral margin of the squamosal and supratemporal (internus), and the posterolateral margins of the supratemporal parietal, and muscle fascia (externus). Both branches extend ventrally overlapping each other to insert on the retroarticular process.

2- Cervicomandibularis

It originates in a wide band from the muscle fascia of longissimus capitis 1, and inserts on the posterior side of the articular (posterior to depressor mandibulae).

3- Constrictor colli

A flat muscle that runs around the neck region (C1-6) (plate 7.4.1c). It extends anteriorly (Rieppel, 1980) and attaches on the lateral side of the paroccipital process, and to the muscle fascia of longissimus capitis 1 and splenius capitis.

4- Trapezius

It originates from the mid-dorsal line, and inserts on the suprascapula (plate 7.4.1c).

5- Latissimus dorsi

See chapter 1.

Intermediate muscles

1- Episternocleidomastoid

It originates from the anterolateral margin of the clavicle, and anteriorly extends along C1-6 to insert laterally on the paroccipital epiphysis.

2- Clavicle dorsalis

Absent.

3- Levator scapulocoracoid dorsalis and ventralis

Both branches originate from the atlas transverse process, and insert on the anterior edges of the suprascapula (dorsalis) and scapulocoracoid (ventralis).

4- Rib to suprascapula/scapulocoracoid muscle slips

The superficial first, second and third cervical rib muscle slips insert on the suprascapula dorsally, while the third and fourth cervical rib muscle slips

insert on the suprascapula posteriorly. The first trunk rib muscle slips insert on the scapulocoracoid posteriorly (plate 7.4.3b).

Deep muscles

1- Obliquus capitis

It originates from the axis neural spine, and inserts on the dorsolateral side of the paroccipital process.

2- Rectus capitis

It originates from the atlas and the anterodorsal process of the axis (spine), and inserts on the dorsolateral surface of the supraoccipital.

3- Splenius capitis

It originates from the muscle fascia of longissimus dorsi above the C3-8 neural spines. The muscle branches anteriorly from longissimus capitis 1 along C3-4, and continues anteriorly to end on the concave posterodorsal edge of the parietal.

4- Spinalis/semispinalis muscles

a) Spinalis capitis

The muscle originates from the C3 neural spine, and extends anteriorly along the axis and atlas to insert on the parietal under the splenius capitis insertion.

b,c) Spinalis and semispinalis cervicus and complex

See chapter 1 (plate 7.4.3c).

5- Longissimus muscles

a)Longissimus capitis 1

Branches from the longissimus dorsi dorsally (above C5), and inserts on the dorsolateral margin of the parietal (plate 7.4.2a) (shallow concave rim).

b) Longissimus capitis 2

Branches from the longissimus dorsi laterally (above C4), and inserts on the lateral edge of the paroccipital process (plate 7.4.2c).

c) Longissimus capitis 3

Absent.

d) Longissimus capitis 4

Branches laterally from the longissimus dorsi, and inserts on the ventrolateral margin of the oto-occipital (crista tuberalis) (plate 7.4.2d).

e) Longissimus cervicus

See chapter 1.

f) Longissimus capitis minor

Branches from longissimus cervicus laterally, and extends dorsally to insert in a ventrolateral fossa on the paroccipital process, internal to the longissimus capitis 2 insertion, and dorsal to longissimus capitis 4 (plate 7.4.2c).

6- Iliocostalis muscles

a) Iliocostalis major

See chapter 1.

B) Iliocostalis cervicus

Absent.

7- Longus muscles

a) Longus colli

Originates centrally from the 7th hypapophysis (of vertebra 6) (plate 7.4.4c), and extends anteriorly receiving slips from the large distal hypapophyses. The muscle inserts laterally on the elongated epiphyses of the basal tubera as a curved tendon (plate 7.4.4b).

b) Longus cervicus

This long tendinous long band originates from the D2 rib (ligament and distal end) and receives a series of tendinous slips from the hypapophyseal lateral distal epiphyses = lateral bundles, and the intercentral apices (2-6) = middle bundle (plate 7.4.5b). The lateral tendons start obliquely from C6-D2 rib ligaments and ribs to end on 2-9 hypapophyseal apices. The longus cervicus inserts finally on the posterior process of the second hypapophysis and the lateral crests (> shaped). The longus cervicus is reduced (narrow tendons) but is longer than longus colli.

8-First hypapophysis to basioccipital muscle

Ventrally, the first hypapophysis muscle extends anteriorly to insert flat on the basioccipital deep to the longus colli insertion (plate 7.4.4d).

9- Posterior (2-3) hypapophyses muscle slips to oto-occipital

Ventrally, the 2nd and 3rd hypapophyseal muscle slips extend to a wide insertion on the convex ventrolateral margin of the oto-occipital (at the same level as the first hypapophysis muscle slip insertion) deep to the longissimus capitis 4 insertion (plate 7.4.4d).

Very deep muscles

1- Deep (4-7) hypapophyses apices muscles

These very deep muscles attach to the centra directly. The longer muscle connects laterally between the 4th and 7th hypapophyses, while the shorter muscle slips run from the 4th hypapophysis distal epiphysis to the distal end of the 5th hypapophysis, and the same applies for the 5th and 6th, and 6th and 7th hypapophyses.

2- Interspinalis, interneural arches and interzygapophyses

See chapter 1.

Special deep and very deep ventral muscles in *Varanus doreanus* and *Varanus jobiensis*

In these two species of *Varanus*, after removing the longus colli, deep muscles running from the hypapophyses to the skull were seen anteriorly, while intercentral muscles to scapulocoracoid and clavicle were seen posteriorly (hypapophyses 4-7) (plate 7.4.5a). After removing the hypapophyses to scapulocoracoid and clavicle muscle, very deep hypapophyses (4-6) to suprascapula (anterior side) muscle slips were observed (plate 7.4.5a). The hypapophyses (4-7) muscles originate from the lower edge of the lateral distal epiphyses, and insert on the anterior edge of the scapulocoracoid and clavicle. The deep hypapophyses (4-6) muscles originate from the lateral side of the deep hypapophyses, and insert on the anterolateral side of the suprascapula. In addition, muscle slips from the first and second cervical ribs insert on the dorso-medial side of the suprascapula (see the intermediate rib to suprascapula/scapulocoracoid muscle slips). The muscles were not examined in *Varanus griseus*.

Comparison of the osteological and muscular features within Varanidae

A comparison of the neck anatomy between *Varanus doreanus, Varanus griseus* and *Varanus jobiensis* (dissected); *Varanus gilleni* and *Varanus prasinus* (skeleton) shows similarities and variation.

1) Similarities between varanids examined:

Excluding general similarities found in other lizards.

- Paroccipital epiphysis is present.
- There are 9 cervical vertebrae, and 10 hypapophyses (sutured to the centra). The hypapophyses are deep with a special lateral and central distal epiphyses (where ventral muscles originate).

- First rib starts on C6 or C7.
- Interclavicle is T- shaped.
- Depressor mandibulae internus originates from quadrate, while the externus originates from supratemporal, parietal and muscle fascia.
- Constrictor colli originates from the muscle fascia dorsally and the paroccipital process laterally.
- Trapezius inserts on the suprascapula.
- Episternocleidomastoid originates from the clavicle, and inserts on the paroccipital epiphysis.
- The rib to the suprascapula deep muscle slips are absent.
- Splenius capitis originates from muscle fascia of longissimus dorsi, and extends superficial to the cervical spines. It branches to longissimus capitis 1 before insertion.
- Spinalis capitis originates from anterior cervical spines.
- Longissimus capitis 4 inserts laterally on the crista tuberalis of the oto-occipital.
- The longissimus capitis minor inserts dorsally on the paroccipital process (beside the longissimus capitis 2, and dorsal to capitis 4).
- Longus colli originates from the hypapophyses. It inserts on the elongated epiphysis of the basal tubera as a curved tendon.
- Longus cervicus is tendinous (reduced), and extends as a series of long narrow tendon slips that connect the ribs to the hypapophyses (distal epiphyses + middle intercentral plates). It is longer than longus colli and begins from dorsal centra.

- Posterior hypapophyses muscle slips insert broadly on the ventrolateral margin of the oto-occipital beside the crista tuberalis. They insert at the same level as the first hypapophysis muscle.
- Hypapophyses to suprascapula muscle slips originate from hypapophyses 4-6.
- Hypapophyses to scapulocoracoid and clavicle muscle slips originate from hypapophyses 4-7.

1) Variation between examined varanids:

- Postzygapophyses have posterior processes (*V. griseus, V. jobiensis* and *V. prasinus*), or tubercles (*V. doreanus*), or are sometimes smooth (*V. gilleni*).
- There are 10 hypapophyses in *V. griseus, V. doreanus, V. jobiensis* and *V. prasinus*, but 9 hypapophyses in *V. gilleni*.
- The rib ratio = 5+2+2 in *V. griseus* and *V. gilleni*, while in *V. doreanus, V. jobiensis* and *V. prasinus* rib ratio = 6+3.
- Depressor mandibulae externus originates from the skull roof and muscle fascia of longissimus capitis 1 (*V. griseus*), or muscle fascia of splenius capitis (*V. doreanus*). The muscle was not investigated in *V. jobiensis*.
- Spinalis capitis originates from C1-3 (*V. griseus*), or C1-4 (*V. doreanus*). The muscle was not investigated in *V. jobiensis*.
- The insertion of longus colli on basal tubera is a strongly curved tendinous bundle in *V. griseus* and *V. doreanus*, while in *V. jobiensis* it inserts as a straight tendinous bundle.
- The number of posterior hypapophyses muscle slips to the skull is 2 in *V. griseus* and *V. doreanus*, but 3 in *V. jobiensis*.

Comparison of osteological and muscular features within Anguimorpha

Table (7.5a) Osteology

Family name / Bone features	Varanidae	Helodermatidae	Xenosauridae	Limbed Anguidae
Paroccipital epiphysis	Present	Absent		
Axis anterior intercentrum	Keeled	Flat	Keeled	
Axis posterior intercentral lateral crests	Absent		Present (large)	Absent
Number of cervical vertebrae	9	8		
Number of intercentra	9-10	4 (reduced)	5	5-7
Centra after last intercentrum	Smooth			Keeled
Intercentral lateral crests	Absent		Present	Absent except 4th intercentrum
First cervical rib starts on	C6 or 7	C4		
Interclavicle shape	T- shape	Cruciform		

Table (7.5b) Myology

Family name / Bone features	Varanidae	Helodermatidae	Xenosauridae	Limbed Anguidae
Depressor mandibulae internus origin	Quadrate	Not observed	Quadrate + squamosal	
Depressor mandibulae externus origin	Supratemporal + parietal + muscle fascia	Not observed	Supratemporal + muscle fascia	Supratemporal + parietal + muscle fascia
Trapezius insertion	Suprascapula	Not observed	Scapulocoracoid	
Constrictor colli insertion	Paroccipital process + muscle fascia	Not observed	Muscle fascia	
Episterno-cleidomastoid origin	Clavicle	Not observed	Interclavicle	
Episterno-cleidomastoid insertion	Paroccipital epiphyses	Paroccipital process		
Splenius capitis extends superficial to	Cervical neural spines	Not observed	Dorsal & cervical neural spines	Not observed
Splenius capitis insertion	Branches to longissimus capitis 1	Not observed	Branches to longissimus capitis 1	Undivided during insertion
Spinalis capitis origin	Anterior cervical spines	Not observed	Posterior cervical spines	Not observed
Longissimus capitis 4 insertion	Crista tuberalis	Not observed	Basal tubera	Ventrolateral end of oto-occipital (convexity)

Family name / Muscle features	Varanidae	Helodermatidae	Xenosauridae	Limbed Anguidae
Longissimus capitis minor insertion	Dorsally on paroccipital process	Not observed	Crista tuberalis	Ventrolateral margin of oto-occipital
Intercentra to scapulocoracoid and clavicle	Present 4-7 intercentra	Absent		
Intercentra to suprascapula	Present 4-6 intercentra	Absent	Absent	Absent or present (*Diploglossus*)
Intercentra to posterior cervical rib muscles	Absent			Absent or present (*Diploglossus*)
Longus colli origin	7th intercentrum (C6)	C8 middle centrum		C8 anterior centrum or D2 centrum (*Diploglossus*)
Longus colli tendon of insertion	Present		Absent	Present
Longus colli extension	Single bundle	Wide single bundle	Divided into 3 sections	Wide single bundle
Longus colli insertion on basal tubera	Curved tendon bundle	Straight wide tendon		
Longus cervicus	Reduced (long oblique tendon bundles)	Reduced (3 short oblique muscle bundles)	Reduced (3 short oblique tendon bundles)	Reduced (one tendon)
Longus cervicus starts from	D2 rib	C8 rib	C5 rib	
Posterior intercentral muscle slips to skull insertion	Oto-occipital	Oto-occipital + basioccipital	Basioccipital	Oto-occipital
Number of posterior intercentral muscle slips to skull	3	1	2	3
Position of posterior intercentral muscles (ventrally)	Same level as 1st intercentral muscle	Superficial to 1st intercentral muscle	Deep to 1st intercentral muscle	
Cervical and trunk central ventral tendon	Absent	Absent	Absent	Present

Common craniocervical features in Anguimorpha

Osteology

1- Squamosal dorsal process is absent (narrow posterior end).

2- Intercentra are fused to the centrum in front.

Myology

Includes data from a full dissection of *Elgaria, Ophiodes, Shinisaurus* and *Varanus*. In *Anguis* and *Heloderma* only the ventral deep muscles were examined, while in *Diploglossus*, only some of the intermediate and deep ventral muscles were examined.

1- Depressor mandibulae externus originates laterally from supratemporal (+/- parietal) and muscle fascia.

2- Episternocleidomastoid inserts on the braincase only.

3- Deep rib to suprascapula muscle slips are absent.

4- Clavicle dorsalis is absent (except *Ophiodes*).

5- Splenius capitis originates from muscle fascia of longissimus dorsi superficial to neural spines.

6- Longus colli has a ventral midline origin from centra and intercentra.

7- Longus cervicus is reduced in all anguimorphs with well-developed limb. The muscle begins laterally from ribs and/or rib ligaments.

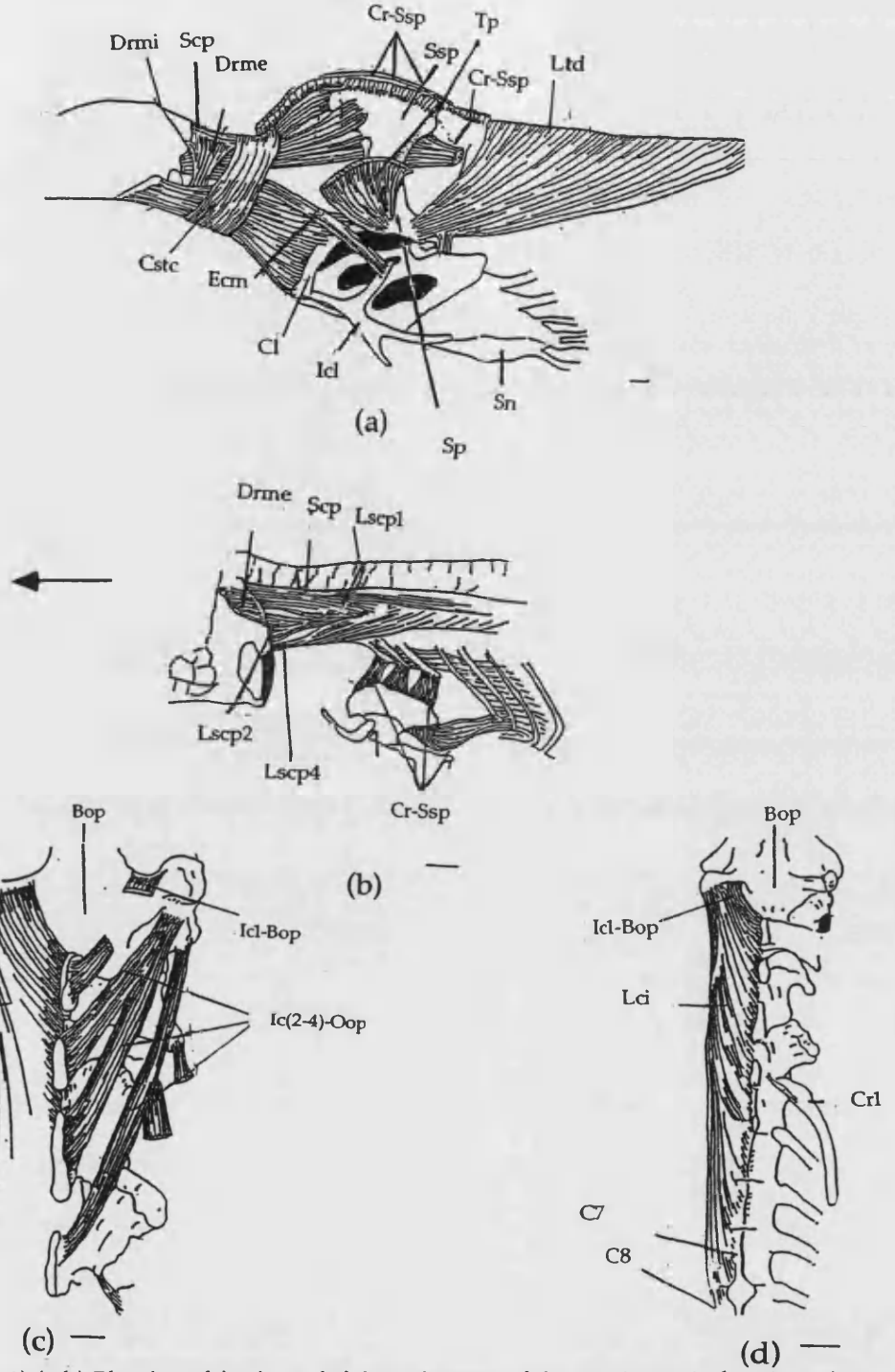


Plate (7.1.1) (a-b) *Elgaria multicarinata*, left lateral views of the craniocervical region, a) most superficial, intermediate and deep muscles including depressor mandibulae (Drme,i), constrictor colli (Cstc), splenius capitis (Scp) and episternocleidomastoid (Ecm) originating from the interclavicle, while clavicle dorsalis (Cld) is absent; b) rib to suprascapula muscle slips (Cr-Ssp), and the extension of deep longissimus capitis 1, 2 and 4 (Lscp1,2 & 4). (c-d)Ventral view of the craniocervical region, c) 1-4 intercentral muscle slips insert on the basioccipital (Bop) and oto-occipital (Oop) (Ic-Bop and Ic[2-4]-Oop); d) start of longus colli (Lci) from C8 and insertion of 1st intercentral muscle slip on the basioccipital (Ic1-Bop). Scale bar = 1 mm.

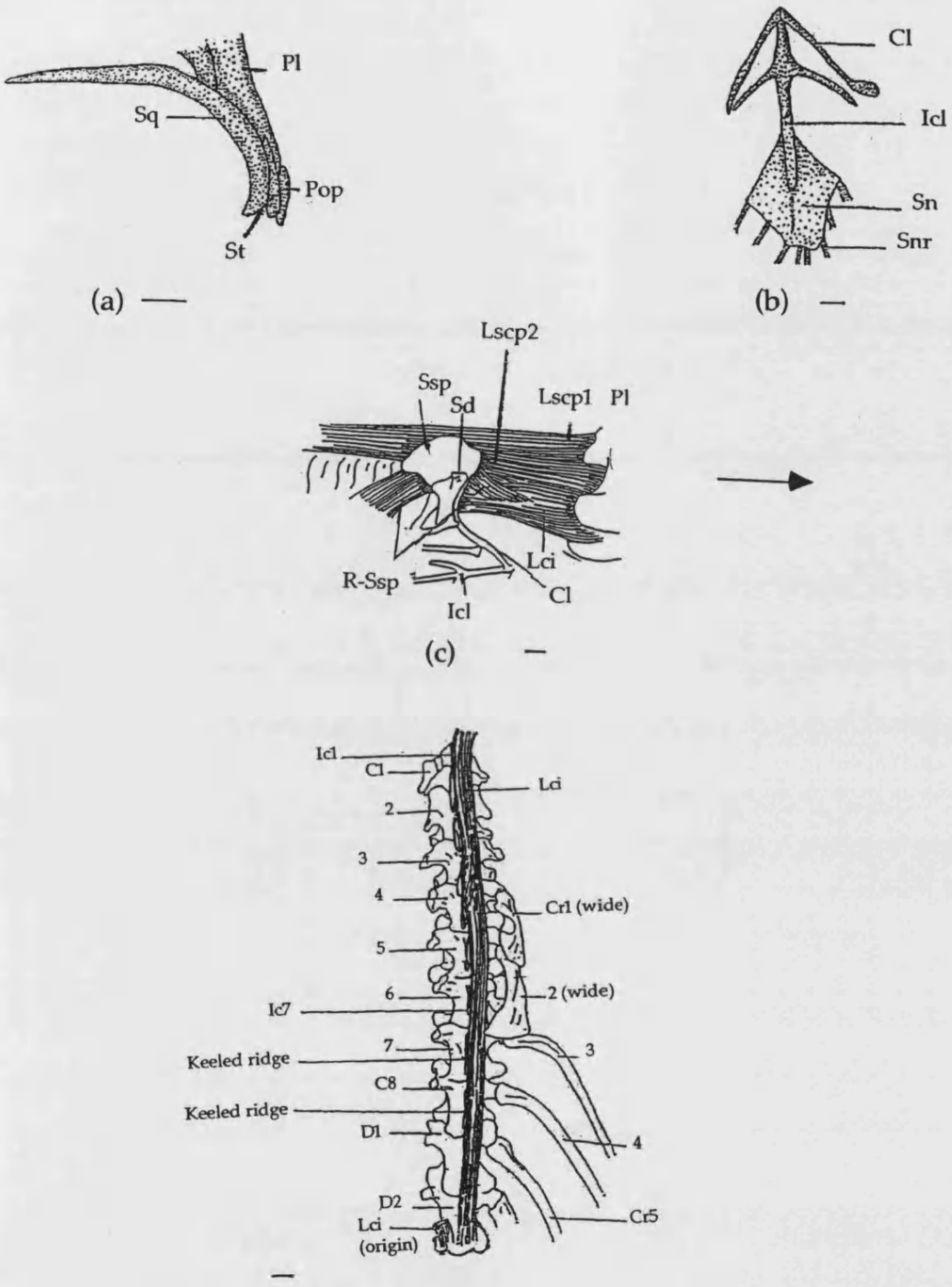
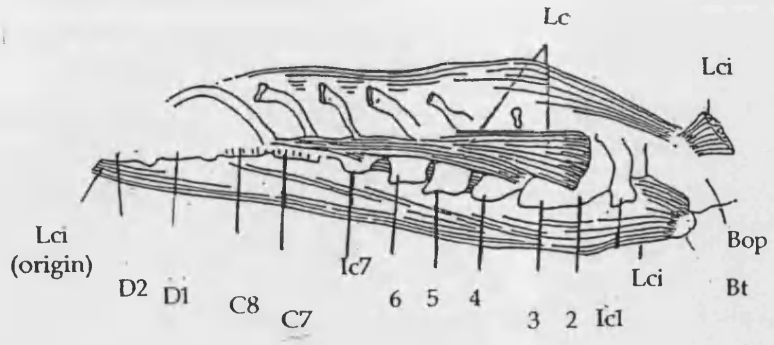


Plate (7.1.2) *Diploglossus monotrofis*, a) left lateral view of the skull showing the position of lateral skull components, squamosal (Sq), supratemporal (St), parietal and part of the paroccipital processes (Pop); b) ventral view of the pectoral girdle showing the cruciform interclavicle (Icl). *Diploglossus c. crusculus*, c) right lateral and posterolateral view of the pectoral girdle muscles with rib to suprascapula and scapulocoracoid muscle slips (R-Ssp/Sd); d) ventral view of the cervical vertebrae shows the origin of longus colli (Lci) from D2, the first and second cervical ribs (Cr1 & 2) are wide distally. Scale bar = 1 mm.



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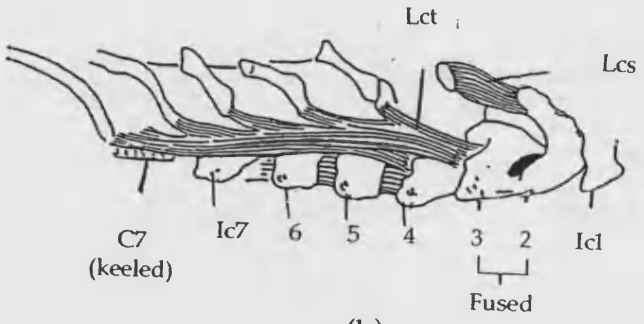

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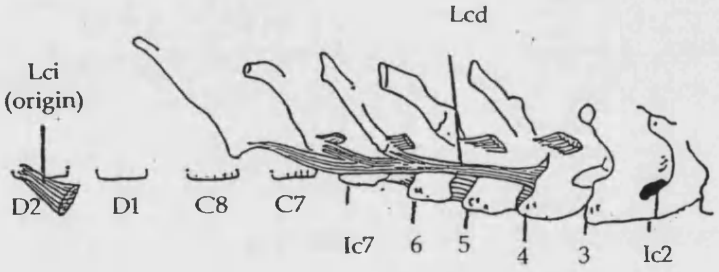

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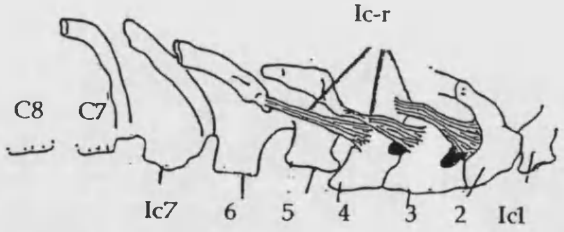


(d)

Plate (7.1.3) *Diploglossus c. crusculus*, right ventrolateral view of the cervical vertebrae showing, a) start of the longus colli (Lci) (D2), longus cervicus (Lc) start (C7); b) the first layer of longus cervicus is removed (superficial = Lcs); c) the second layer of longus cervicus is removed (intermediate = Lct) and longus cervicus deep layer appears (Lcd); d) very deep intercentral muscle slips to ribs (Ic-r). Scale bar = 1 mm.

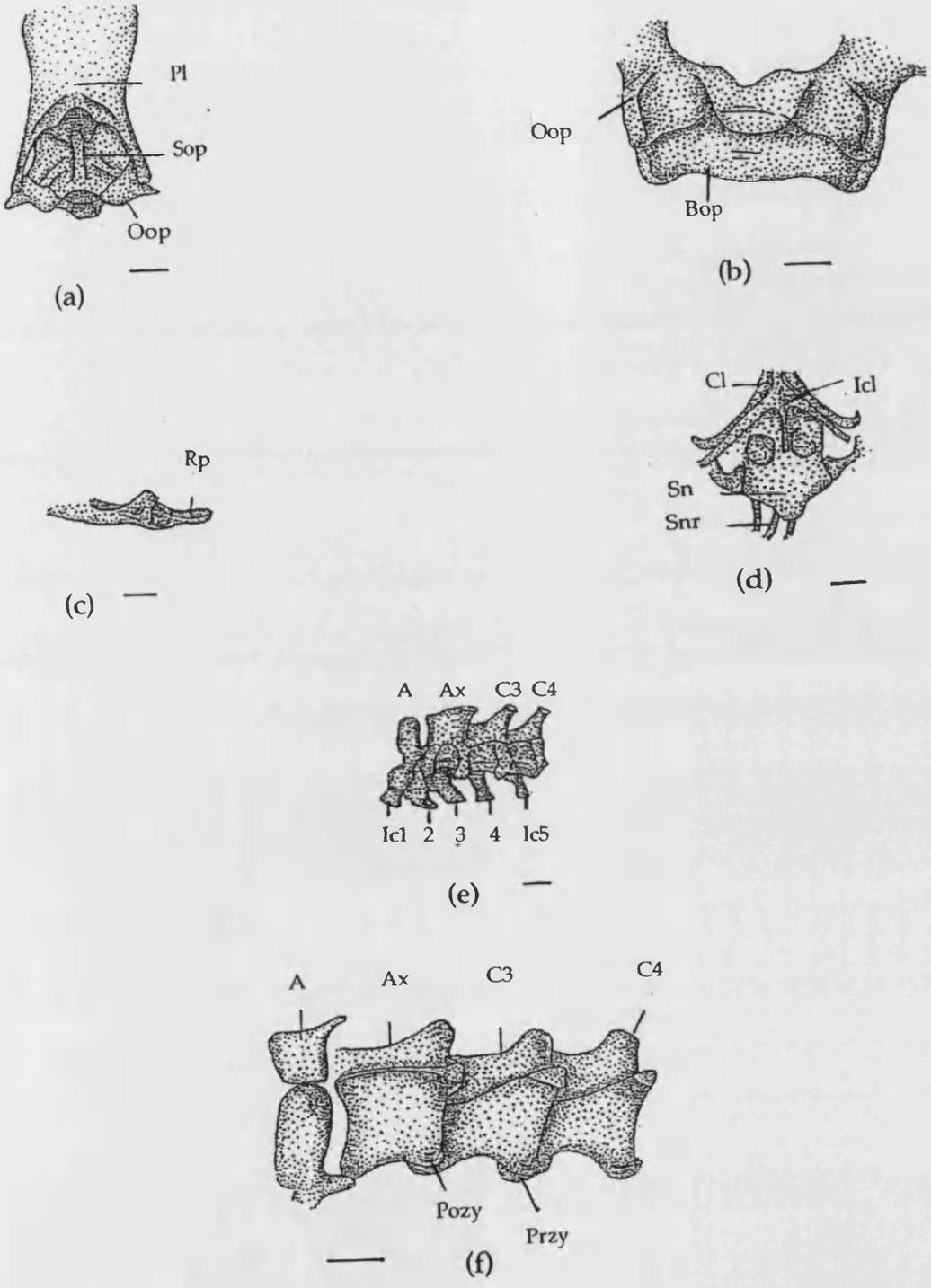


Plate (7.1.4) *Ophiodes striatus* (limbless anguid), a) dorsal view of the parietal (Pl) and braincase; b) occipital view of the skull showing the basioccipital (Bop) and oto-occipital (Oop); c) left dorsolateral view of a well developed retroarticular process (Rp); d) ventral view of the pectoral girdle with cruciform interclavicle (Icl); e) left lateral view of the anterior cervical vertebrae; f) dorsolateral view of the anterior cervical vertebrae showing the postzygapophyses (Pozy) and prezygapophyses (Przy). Scale bar = 1 mm.

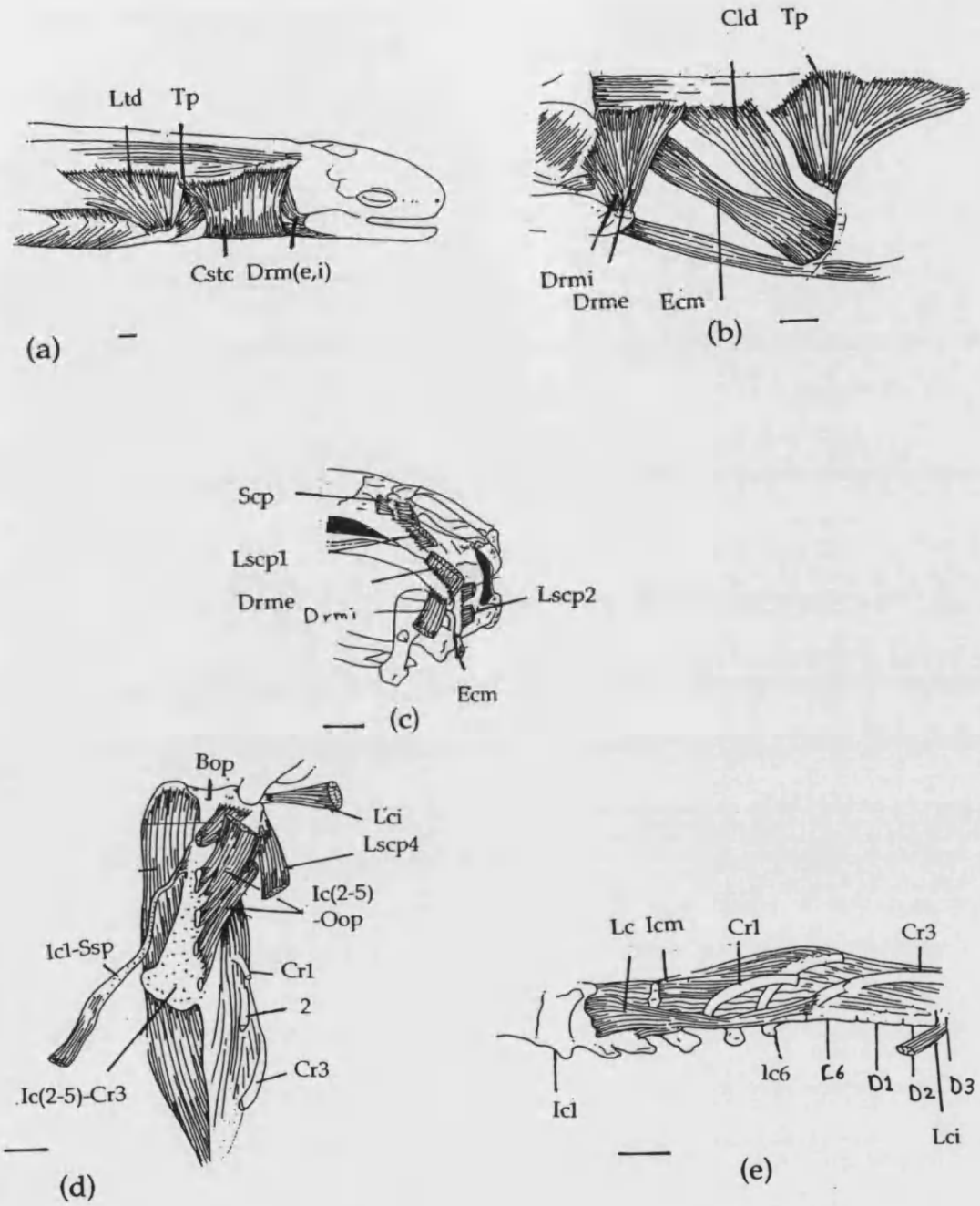


Plate (7.1.5) *Ophiodes striatus*, a) right lateral view of the craniocervical region with constrictor colli (Cstc), trapezius (Tp) and latissimus dorsi (Ltd) muscles; b) left lateral view of the craniocervical region showing depressor mandibulae (Drme,i), clavicle dorsalis (Cld) and episternocleidomastoid (Ecm) muscles; c) left posterolateral views of skull with most superficial, intermediate and deep muscles insertion, splenius capitis (Scp) and longissimus capitis 1 and 2 (Lscp1 & 2); d) ventral view of craniocervical region with longus colli (Lci) and tendinous muscle between the intercentra and suprascapula (Ic1-Ssp), and intercentra to third cervical rib (Ic[2-5]-Cr3); e) left ventrolateral view of the craniocervical region showing longus cervicus (Lc) origin from C6 rib, while longus colli (Lci) originates from D3. Scale bar = 1 mm.

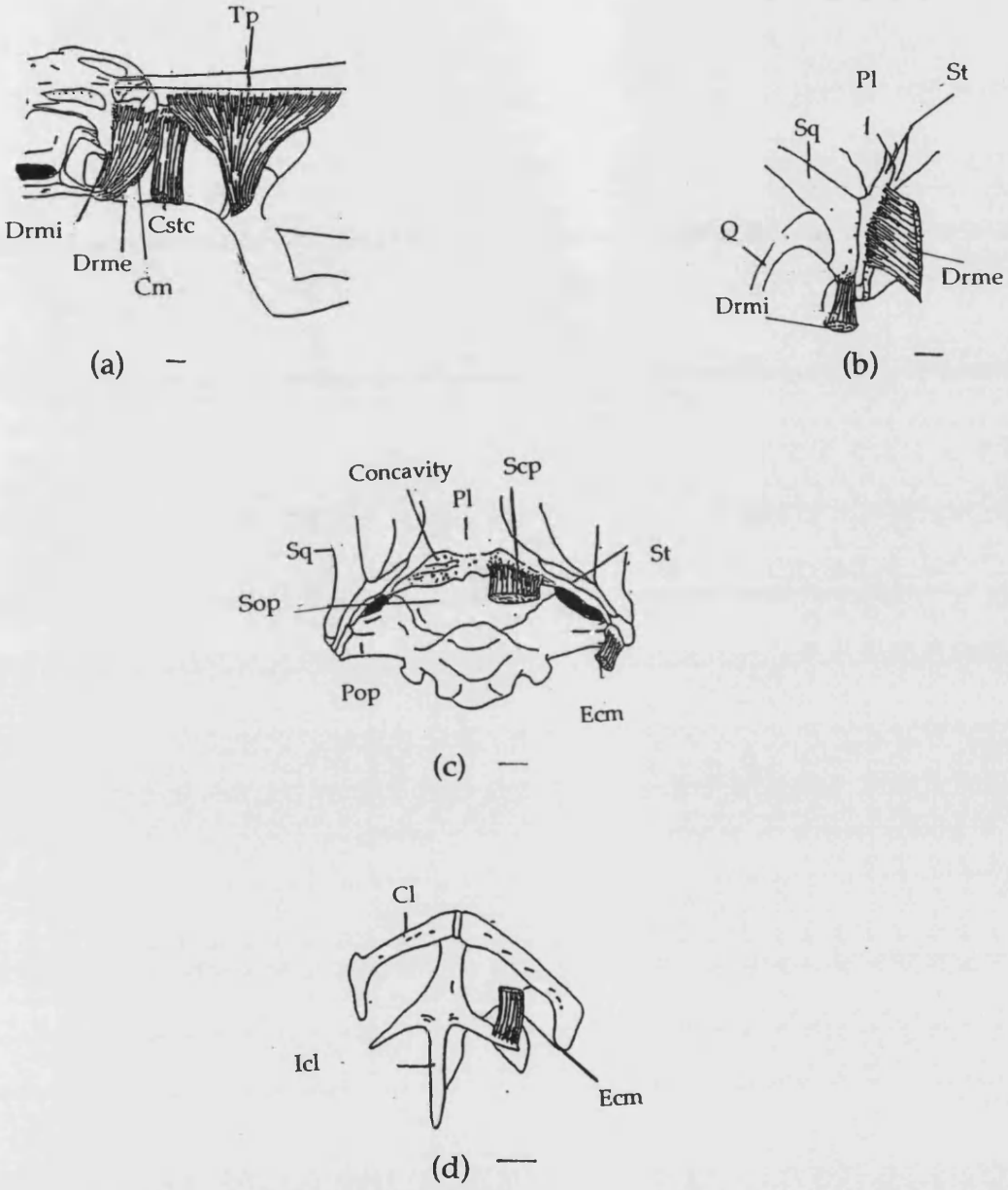
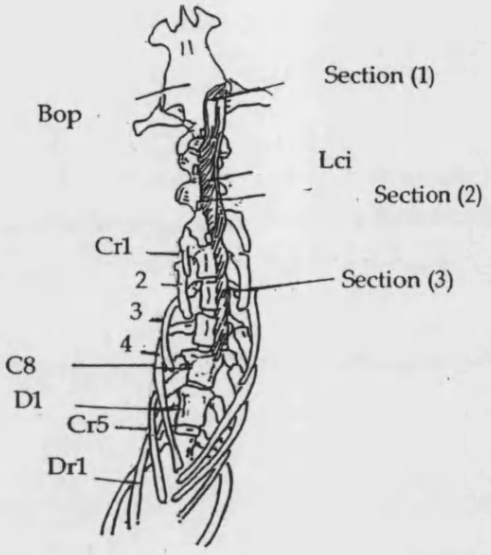


Plate (7. 2.1) a) *Shinisaurus crocodilurus,* a) left lateral view of craniocervical region with most superficial muscles, depressor mandibulae (Drm), constrictor colli (Cstc) and trapezius (Tp); b) left posterolateral view of the skull showing where depressor mandibulae internus (Drmi) originates (squamosal and quadrate) and externus (Drme) originates (supratemporal and muscle fascia); c) posterodorsal view of the skull showing the insertion of splenius capitis (Scp) on the parietal (concavity), while episternocleidomastoid (Ecm) inserts on the paroccipital process; d) ventral view of pectoral girdle showing the origin of episternocleidomastoid (Ecm) from the lateral processes of the interclavicle (Icl).
Scale bar = 1 mm.



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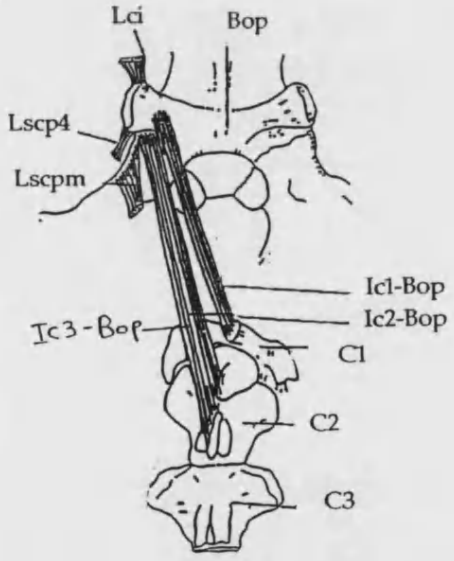

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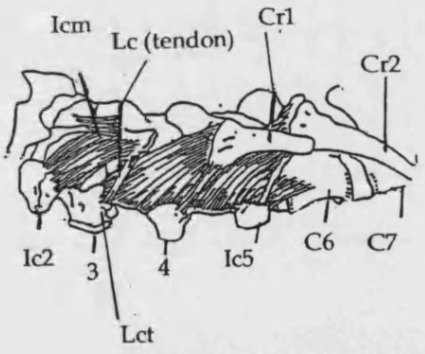

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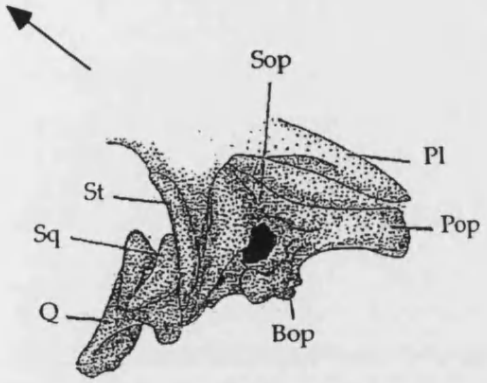
Plate (7.2.2) *Shinisaurus crocodilurus,* a) ventral view of the cervical region where longus colli (Lci) starts from C8; b) ventral view of the craniocervical view showing the insertion of the intercentra 1-3 muscle slips on the basioccipital (Bop); c) left ventrolateral view of the cervical vertebrae showing the tendinous longus cervicus (Lc) (reduced), and very deep intercentral slips to ribs (iliocostalis major) (Icm). Scale bar = 1 mm.



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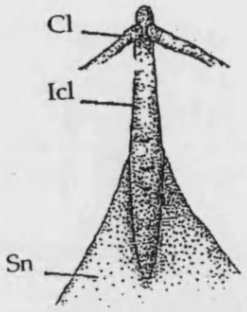

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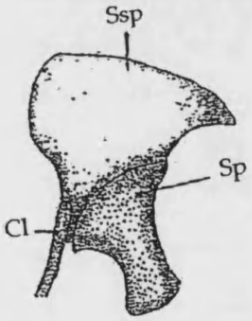
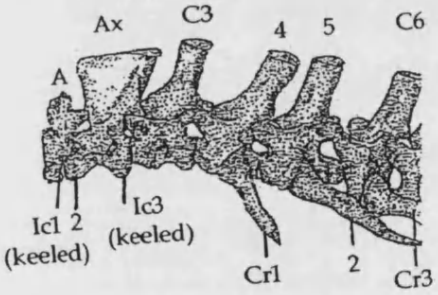


(c)



(d)

Plate (7.3.1) *Heloderma horridum*, a) left posterodorsal view of the skull and braincase, squamosal (Sq) and paroccipital process (Pop); b) ventral view of the pectoral girdle showing the rod-shaped interclavicle (Icl); c) left lateral view of the pectoral girdle showing the clavicle (Cl) articulating with suprascapula (Ssp); d) left lateral view of anterior cervical vertebrae showing the 4 weakly developed intercentra (Ic1-4). Scale bar = 1 mm.

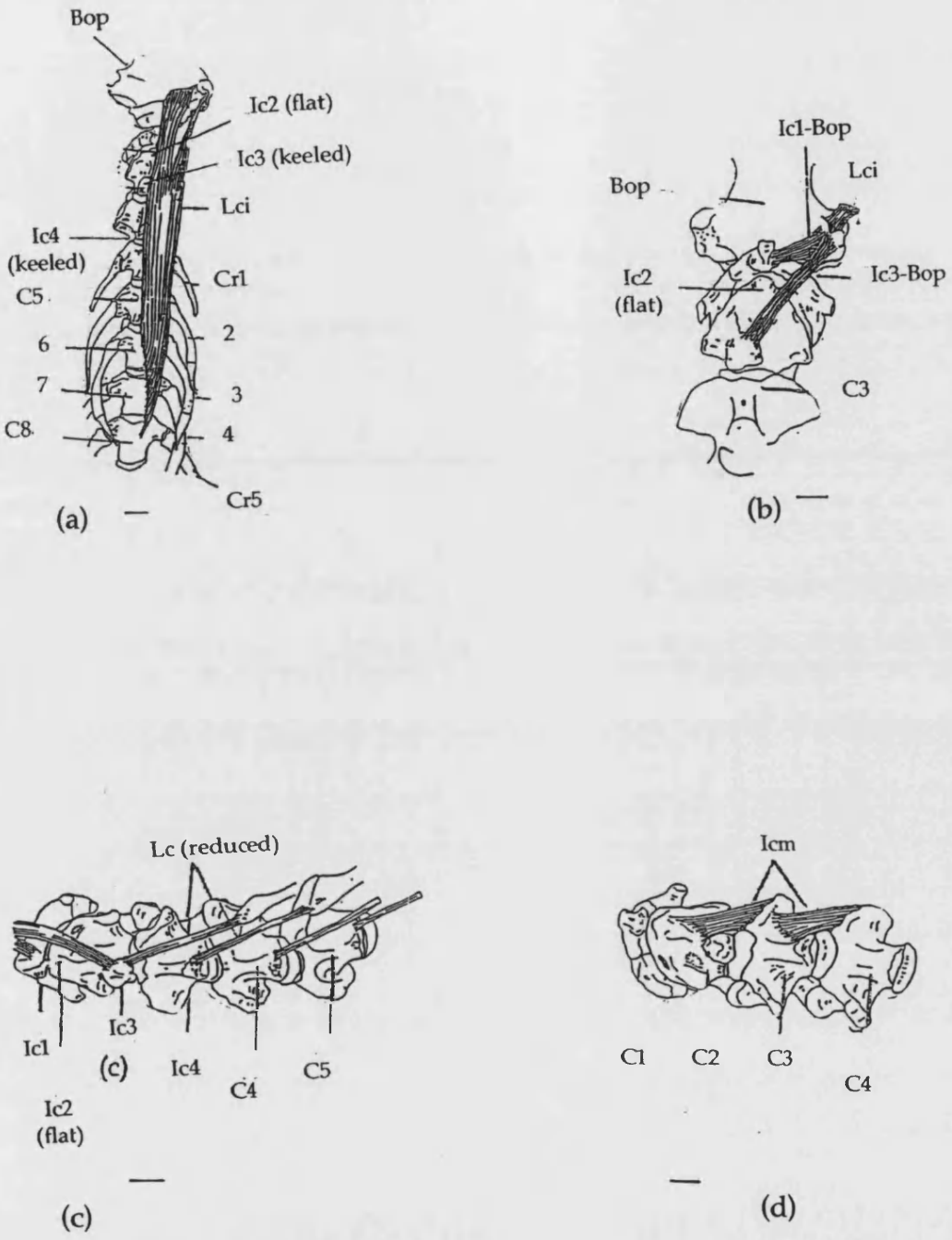


Plate (7.3.2) *Heloderma horridum,* a) ventral view of the craniocervical region shows the origin of longus colli (Lci) (C8); b) ventral view of craniocervical region showing 1st and 3rd intercentral muscle slips to basioccipital (Bop) (Ic1-Bop and Ic3-Bop); c) left ventrolateral view of the cervical vertebrae with short muscle slips from intercentra to ribs (reduced longus cervicus- Lc); d) left ventral view of anterior cervical vertebrae showing very deep ventral slips from intercentra to ribs (iliocostalis major - Icm). Scale bar = 1 mm.

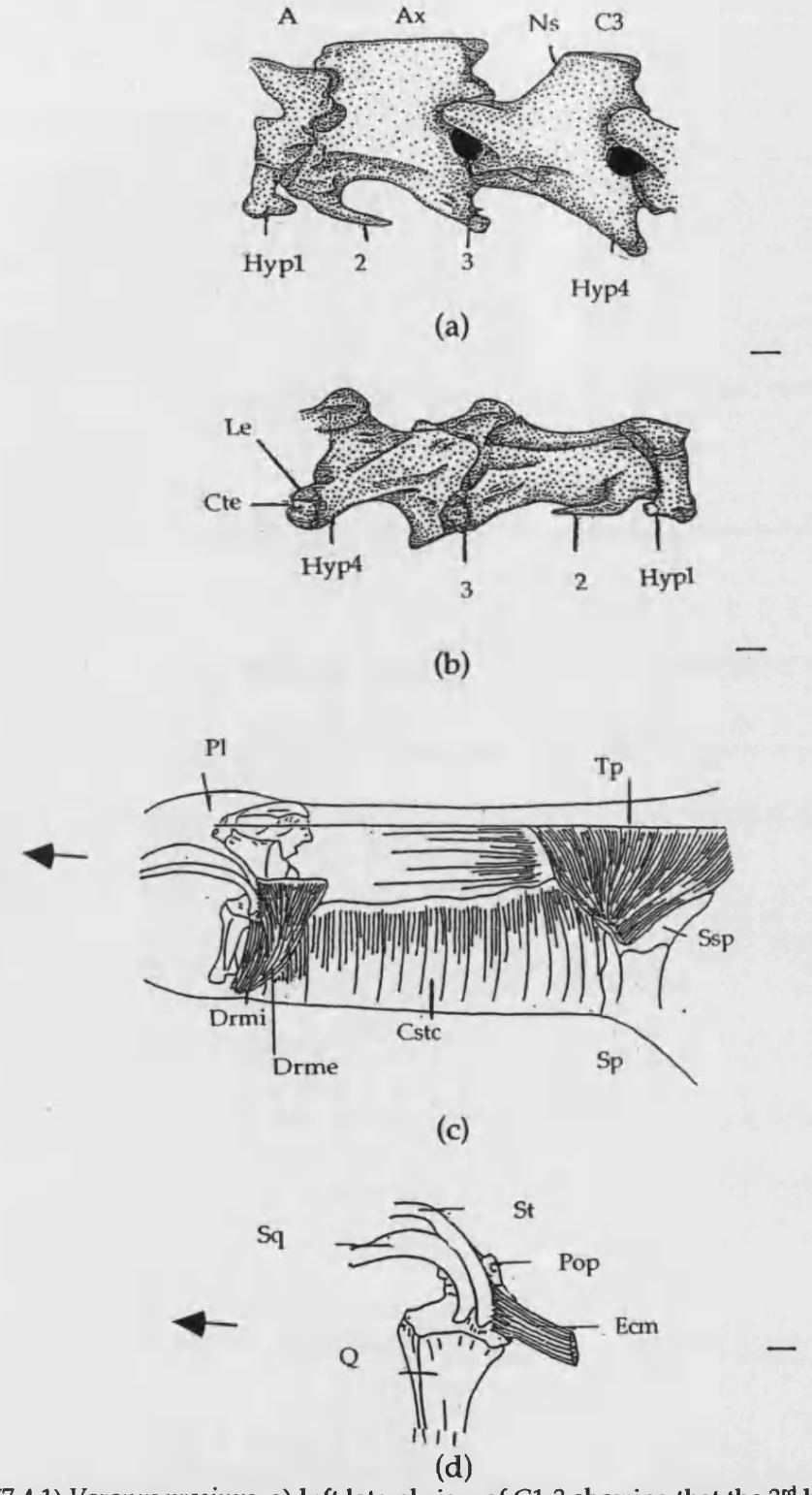


Plate (7.4.1) *Varanus prasinus,* a) left lateral view of C1-3 showing that the 3rd hypapophysis (Hyp3) is fused to the axis (Ax); b) right ventrolateral view of hypapophyses of C1-3 with well-developed apices that bear lateral and central epiphyses (Le & Cte) (where longus colli and cervicus attach); c) left lateral view of the craniocervical region where constrictor colli (Cstc) is wide and originates from parietal and muscle fascia; d) left lateral view of the skull showing the insertion of episternocleidomastoid (Ecm) on the paroccipital epiphyses. Scale bar = 1 mm.

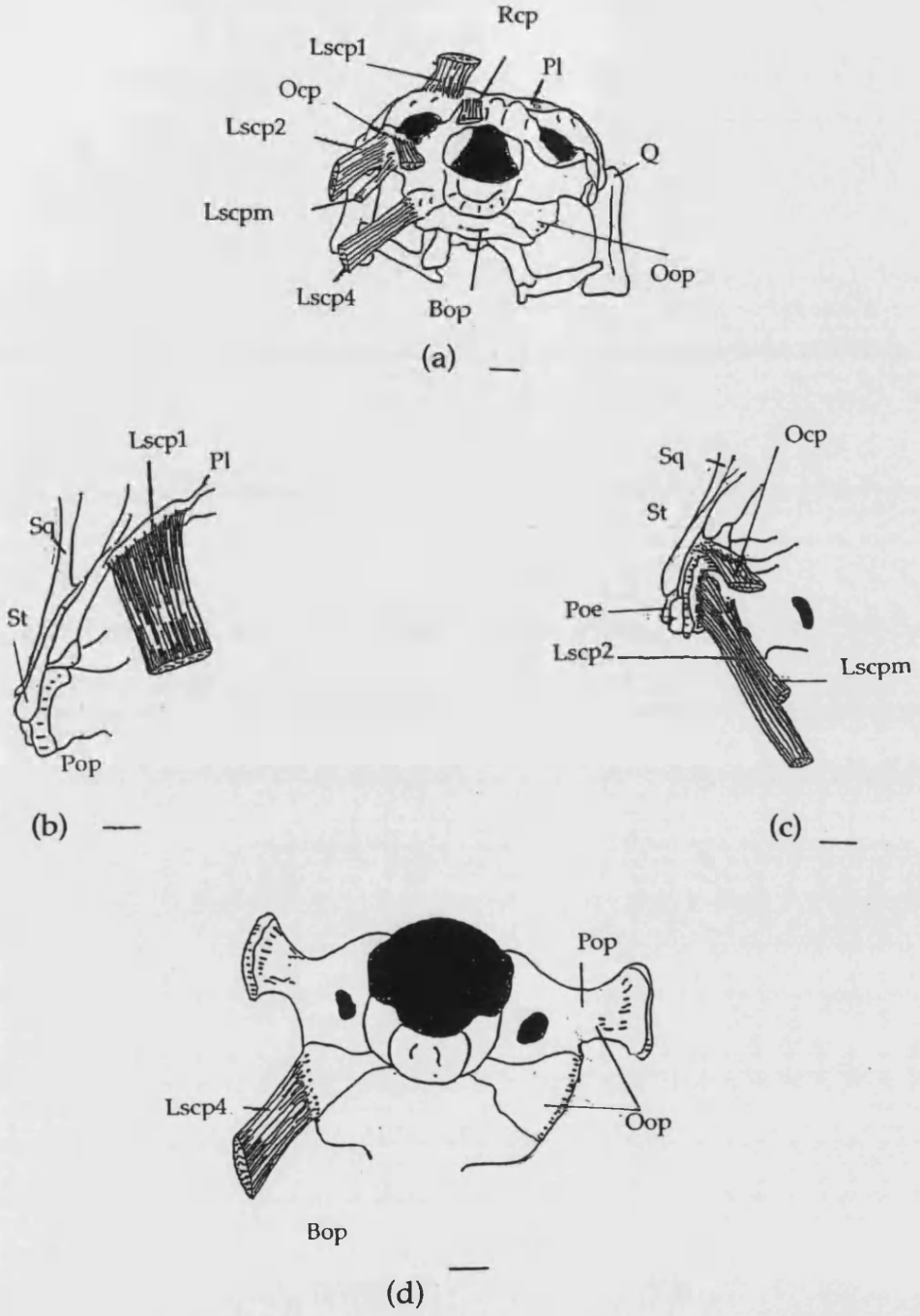


Plate (7.4.2) *Varanus griseus*, a) occipital view of the skull showing most intermediate and deep muscle insertions; b) partial occipital view of the skull showing the insertion of longissimus capitis 1 (Lscp1) on the parietal; c) partial occipital view of the skull showing the insertion of longissimus capitis 2 (Lscp2) and minor (Lscpm), and obliquus capitis (Ocp) on paroccipital process; d) partial occipital view of the skull showing the oto-occipital and basioccipital with wide insertion of longissimus capitis 4 (Lscp4) on the external margin of the oto-occipital. Scale bar = 1 mm.

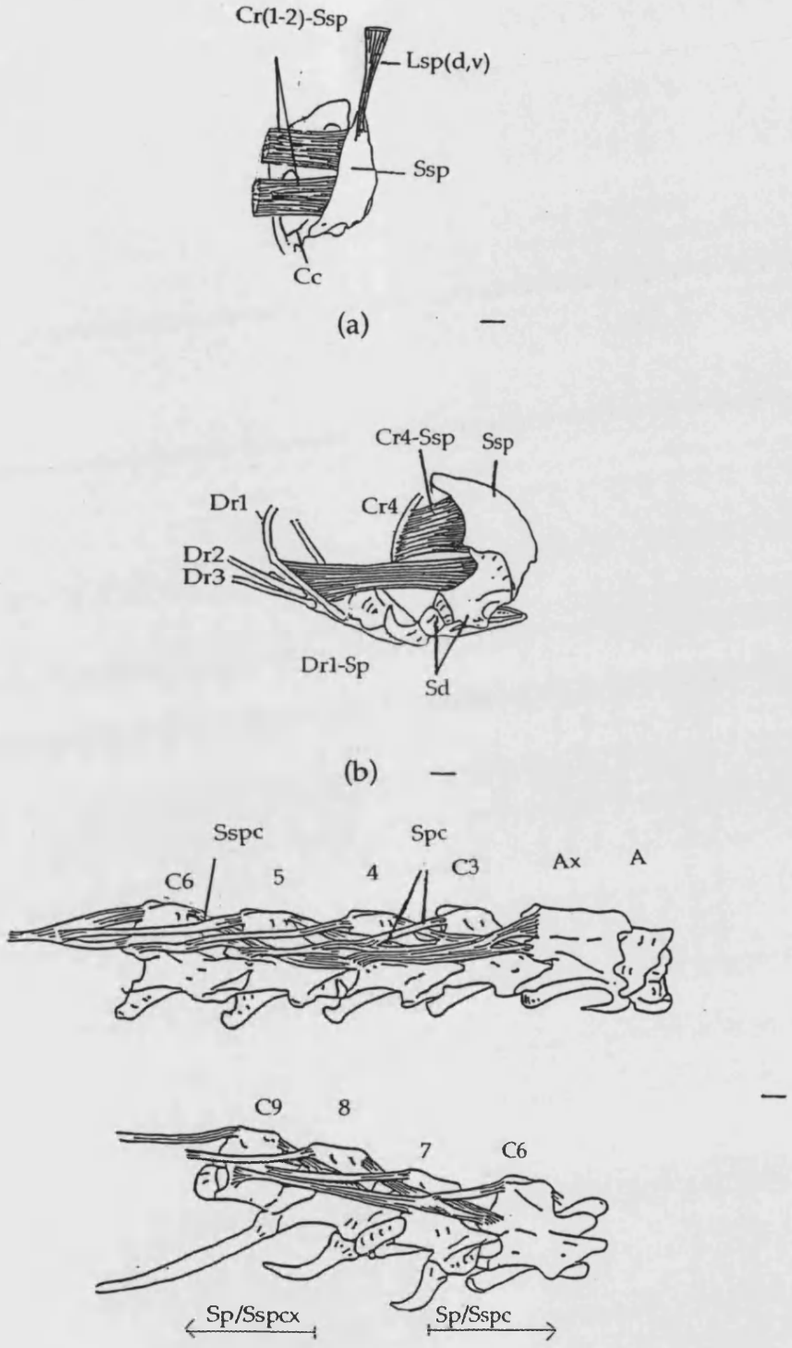


Plate (7.4.3) *Varanus griseus*, a) right ventrolateral view of the pectoral girdle showing the dorsal rib muscle slips to suprascapula and scapulocoracoid (Cr-Ssp/Sd); b, c) right lateral view of the cervical vertebrae with spinalis cervicus (Spc) and spinalis / semispinalis complex (Sspcx) extension. Scale bar = 1 mm.

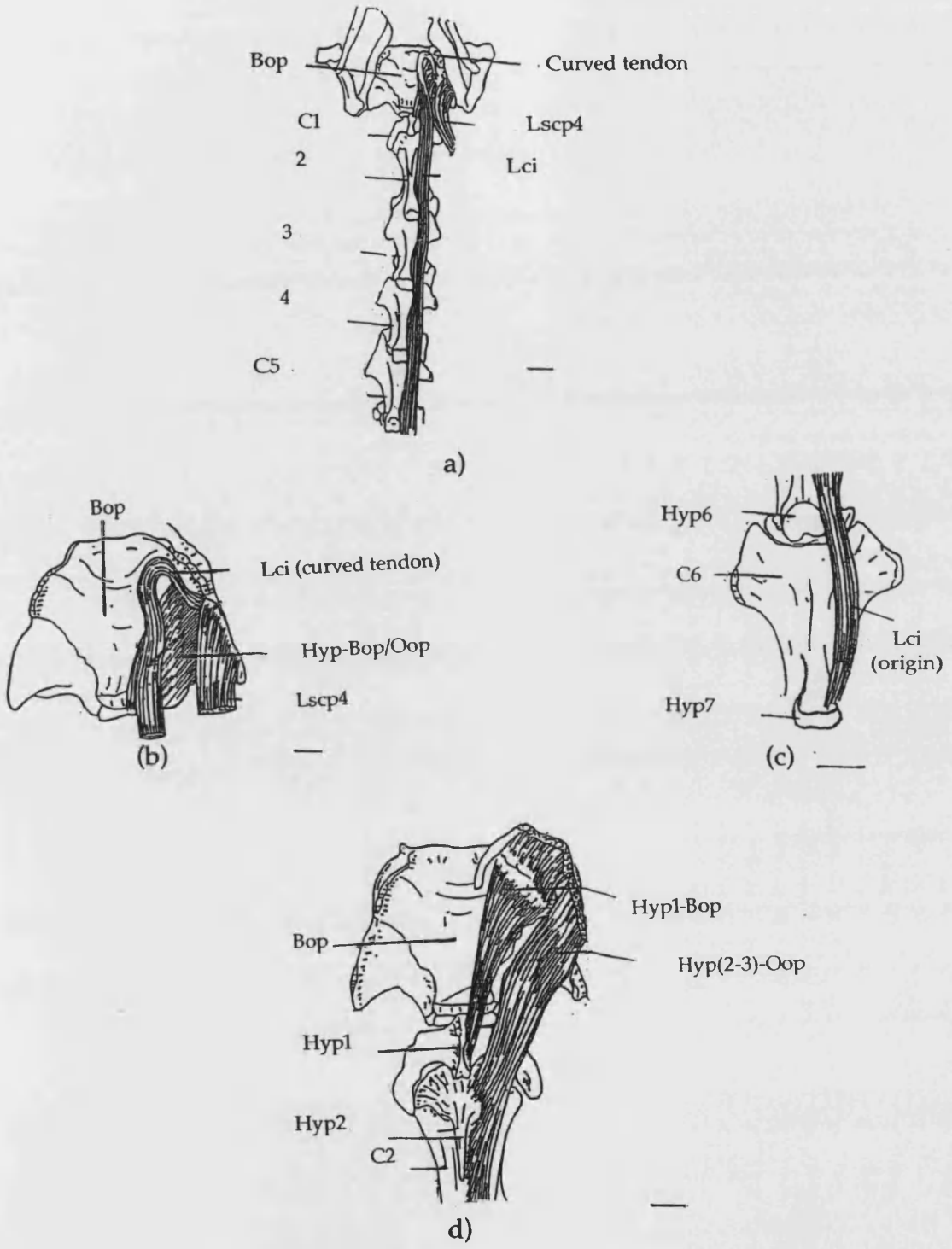


Plate (7.4.4) *Varanus griseus*, ventral view of the craniocervical region a) longus colli (Lci) extension and longissimus capitis 4 (Lscp4) insertion; b) curved insertion of longus colli (Lci) on the basioccipital (Bop); c) start of longus colli (Lci) from C6 and hypapophysis 7; d) 1st hypapophysis to basioccipital muscle (Hyp1-Bop) and 2nd –3rd hypapophyses to oto-occipital muscle slips (Hyp[2-3]-Oop), hypapophyses to skull muscles insert wide and beside each other. Scale bar = 1 mm.

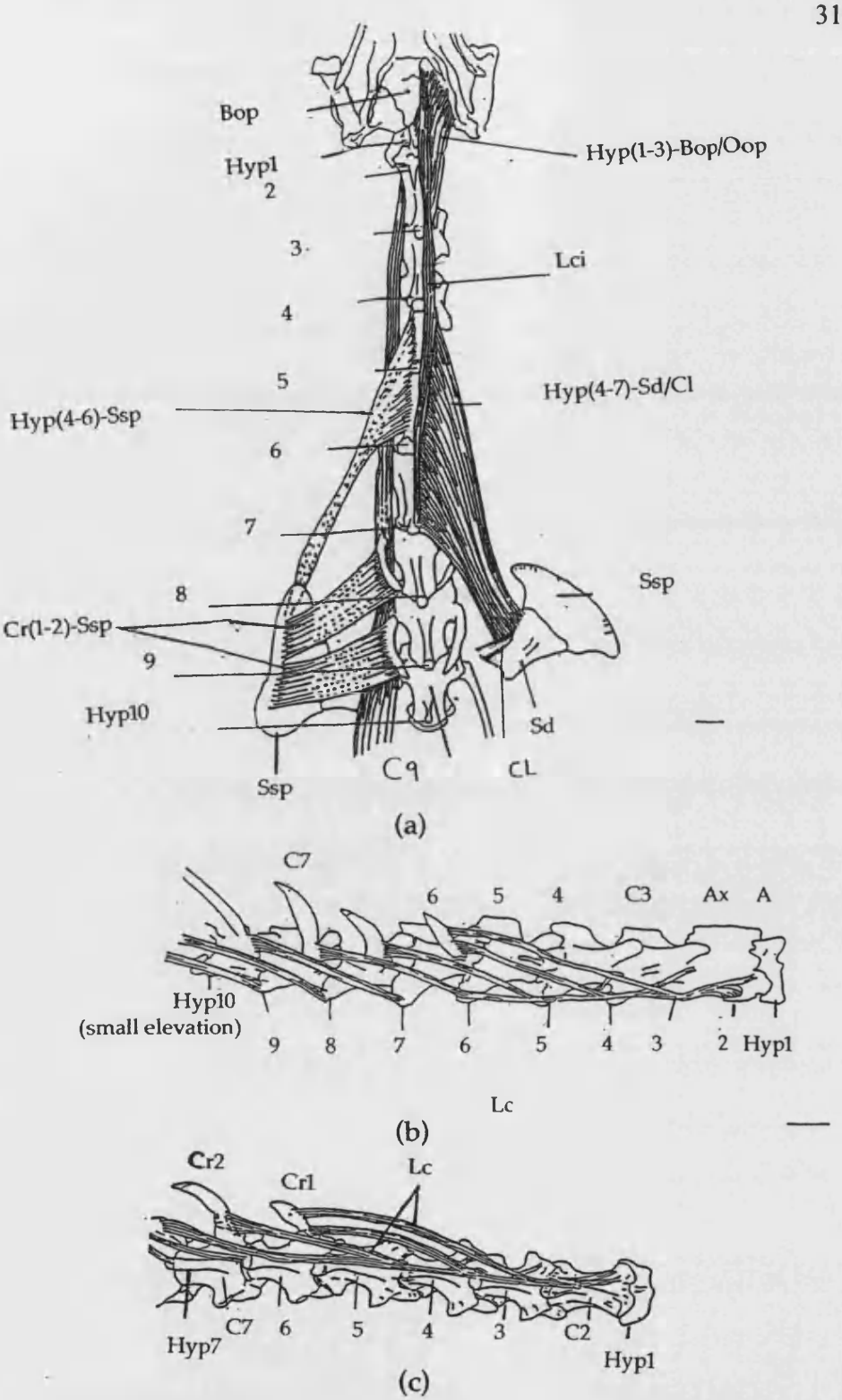
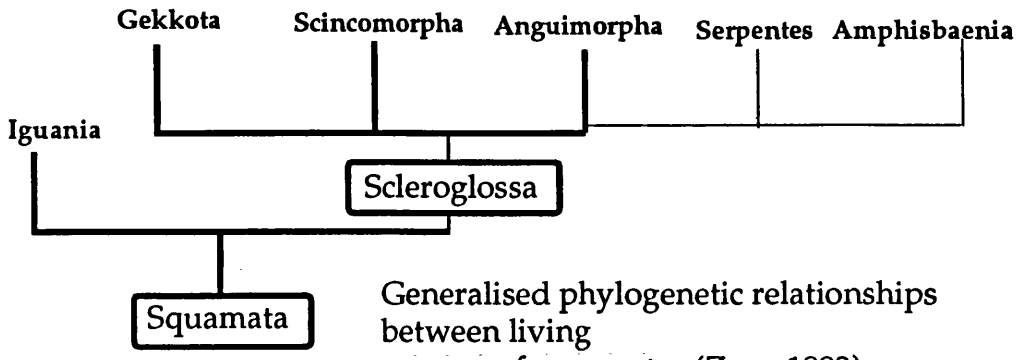


Plate (7.4.5) *Varanus doreanus*, a) ventral view of the craniocervical region with hypapophyses (Hp) to pectoral girdle muscle slips and cervical ribs to suprascapula muscles (Cr-Ssp); b) right lateral view of the cervical vertebrae with tendinous longus cervicus (Lc) origin, extension and insertion; c) right ventral view of the cervical vertebrae with longus cervicus (Lc) tendinous slips from hypapophyses apices and ribs Scale bar = 1mm.

CHAPTER (8)

AMPHISBAENIA

Amphisbaenians are a group of limbless squamates, considered as an independent group within the order Squamata. They are tropical and subtropical fossorial forms with 4 families, 18 genera and 152 species. The Trogonophidae inhabit North Africa and western Iran across the Arabian Peninsula to Aden (e.g. *Diplometopon zarudnyi*). They are modified for digging with a downward pointed tail. The family Bipedidae comprises only the genus *Bipes* which inhabits northwestern Mexico. All species retain short forelimbs that lie far forward, giving the popular name of " little lizard with big ears". The Rhineuridae (e.g. *Rhineura floridana*) was once a widespread group across Florida. The Amphisbaenidae includes 120 diverse species of true amphisbaenians with a specialized tunnel-forming lifestyle (Webb et al., 1978; Young, 1981; Duellman and Heatwole, 1992; Gans, 1992b; Zug, 1993).
They inhabit Africa, South America, Central and North America and Asia, including the Arabian Peninsula (Webb et al., 1978).
Amphisbaenians have been reported from the late Cretaceous (Wu et al, 1993), and are distinguished from other squamates in the following features: the skull is heavily ossified; the scales are small and arranged in rings that encircle the body; and the right lung is reduced rather than the left (limbless lizards and snakes have the left lung reduced).
Amphisbaenians are true burrowers that are well-adapted to an underground enviroment. They have a compact skull, reduced functional eyes, no external ears, and no limbs or girdles (except *Bipes* with well-developed forelimbs, and remnants of the shoulder girdle in the family Trogonophidae). They make tunnels into different types of soil using movements of their heads. (Duellman and Heatwole, 1992; Gans, 1992b).



Generalised phylogenetic relationships between living groups of squamates (Zug , 1993).

In Trogonophidae, the head is twisted and rotated during excavating which results in structural changes like a shaving edge on the skull, anterior intervertebral fusion and a flat cross section of the trunk (Gans, 1969a) . In Amphisbaenidae, the head first moves in the soil, then the head joint is rotated to widen the tunnel. This is reflected by the keeled pointed head, expanded vertebral joints and the more circular cross section of trunk.

Anatomy of the neck region in Amphisbaenia

Family: Trogonophidae.

Diplometopon zarudnyi (Dissected)

Trogonophis wiegmanni (Skeleton)

Previous works:

Cope, 1892; Camp, 1923; Zangerl, 1944, 1945; Kritzinger, 1946; Bellairs and Underwood, 1951; Romer, 1956; Bellairs, 1969; Gans, 1960, 1978; Jollie, 1960; Gasc, 1981; Al-Nassar, 1976; Estes et al., 1988.

Osteology of *Diplometopon zarudnyi*

(Plate 8.1 - 8.2)

Skull

1- Parietal

This is a wide elongated plate that occupies most of the cranial roof. The bone expands ventrolaterally into descending flanges which meet the

paroccipital processes (otic capsule) posterolaterally (Bellairs and Underwood, 1951; Gans, 1960, 1978; Al-Nassar, 1976) (plate 8.1a). The mid-posterodorsal margin of the parietal is not straight or smooth and is fused to the supraoccipital (Zangerl, 1944). This feature is shared with other burrowers like *Dibamus* (Rieppel, 1984), and the pygopodid *Aprasia* (Underwood, 1957).

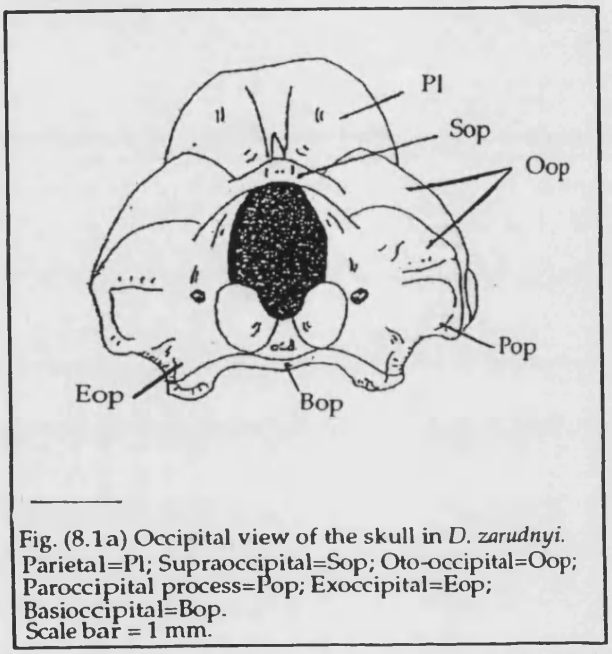


Fig. (8.1a) Occipital view of the skull in *D. zarudnyi*. Parietal=Pl; Supraoccipital=Sop; Oto-occipital=Oop; Paroccipital process=Pop; Exoccipital=Eop; Basioccipital=Bop. Scale bar = 1 mm.

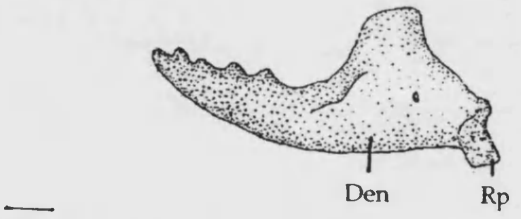


Fig. (8.1b) Left lateral view of the lower jaw showing reduced retroarticular process (Rp) in *Trogonophis wiegmanni*. Scale bar 1 mm.

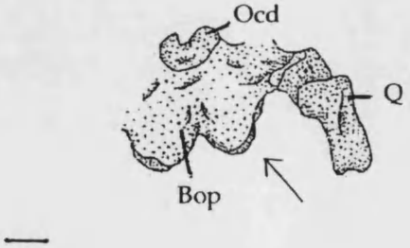


Fig. (8.1c) Occipital view of the skull showing basioccipital with elongated basal tubera (Bt) *T. wiegmanni*. Scale bar = 1 mm.

2-Squamosal

Absent (Romer, 1956) as in *Dibamus* and *Aprasia* (Rieppel, 1984).

3- Supratemporal

This is a small bone which lies between the quadrate and paroccipital process (plate 8.1a) (Kritzinger, 1946; Romer, 1956). Zangerl (1944) interpreted the bone as the squamosal and referred to it as a thin bone with various stages of reduction. He has also repoted the absence of the supratemporal in some amphisbaenians (e.g. *Rhineura*).

4- Quadrate

This square bone takes an oblique to horizontal position as in some fossorial snakes (e.g. Scolecophidia) and in *Bipes biporus* (Zangerl, 1944). The quadrate is firmly connected to the cranial wall, which would limit any streptostylic action (Jollie, 1960) (plate 8.1a).

5- Retroarticular process

The process extends posteroventrally from the concave surface of the articular where the quadrate rests (where depressor mandibulae inserts). (Fig. 8.1b)

6- Supraoccipital

This dorsal median bone is fused with the parietal and the oto-occipital laterally (Gans, 1978) (plate 8.1a, b).

7) Oto-occipital

The oto-occipital is fused to the supraoccipital dorsally, and the basioccipital ventrally. Laterally, the bone are fused to the occipital ring (co-ossified or no boundaries) and form most of the occipital surface of the skull. The paroccipital processes are short (where most deep muscles insert) (Zangerl, 1944; Kritzinger, 1946; Romer, 1956). (Fig. 8.1a)

8) Paroccipital epiphyses

Absent.

9) Basioccipital

This ventral bone is fused with the oto-occipital dorsally and has two basal tubera with elongated narrow epiphyses. (Fig. 8.1c)

Presacral vertebral column

1- Atlas

The posterior process is short, the transverse processes are pointed posteriorly, and the intercentrum is keeled.

2- Axis

The postzygapophyses are horizontal and possess tubercles. The transverse processes are small and project laterally (Zangerl, 1945; Gans, 1960). Ventrally, the anterior intercentrum has lateral crests (where longus cervicus inserts), and the posterior intercentrum is smooth. The posterior intercentrum is fused to the axis (Romer, 1956; Gans, 1960, 1978; Hoffstetter and Gasc, 1969; Al-Nassar, 1976).

3- Cervical and dorsal vertebrae

The cervical region is not differentiated from the trunk region, but there are 10 keeled intercentra (Zangerl, 1945), although Gans (1960) figured 8 intercentra (Fig. 8.2b). Al-Nassar, (1976) describes only atlas, axis and third cervical, while Zangerl (1945) noted 3-5 cervical vertebrae. The centra are procoelous (Cope, 1892; Camp, 1923; Zangeral, 1945; Romer, 1956; Hoffstetter and Gasc, 1969; Gans, 1978).

In *Trogonophis wiegmanni* the tips of the anterior neural spines are compressed and are barely developed, while posteriorly they disappear (plate 8.1d). Dorsally, the width of the neural arches is greater than their length, and laterally the central depth is greater than the length, and the width of the arches is equal to that of the centra.

In *Diplometopon zarudnyi* the tips of the anterior neural spines are compressed but the spines are elongated and more developed with a close arrangement (plate 8.2a). This agrees with Gans (1960, 1978) who differentiates *Diplometopon* from other trogonophids in having high

anterior neural spines which disappear posteriorly along the vertebral column (plate 8.2b). He suggested that this might reduce the dorsoventral flexibility of the anterior spines. In the posterior vertebrae (20~21) the spines and vertebrae become flatter and depressed (low median ridges). This differentiates amphisbaenian vertebra from those of other squamates (Hoffstetter and Gasc, 1969). The anterior margins of the spines are smooth and slightly curved. In the two taxa examined (*Diplometopon* and *Trogonophis*), the postzygapophyses are horizontal and rough. The prezygapophyses have prezygapophyseal processes (Hoffstetter and Gasc, 1969; Gans, 1978) (where the longissimus dorsi muscle slips attach). A ventral keel is absent, and the intercentra are smooth and fused to the centrum in front (Zangerl, 1945; Hoffstetter and Gasc, 1969; Estes et al., 1988).

Ribs

The first short rib is on vertebrae 4 (plate 8.2c) (Bellairs and Underwood, 1951; Gans, 1960; Hoffstetter and Gasc, 1969) and is rounded, smooth and has a pointed end. The anterior ribs are uniformly short and free, but become gradually larger and longer posteriorly (Camp, 1923 - *Amphisbaenia*;). The costal heads have dorsal and ventral pseudotubercula (narrow long posterodorsal process + wide small anteroventral process, asymmetrical) for the attachment of the very deep ventrolateral muscles (Camp, 1923; Zangerl, 1945 - "tendon processes"; Hoffstetter and Gasc, 1969; Al-Nassar, 1976; Gans, 1978; Gasc, 1981 -"M. tuberculocostalis") (plate 8.1c, e). The ribs are connected to the intercentra by ligaments which continue posteriorly by attaching to the transverse processes.

Pectoral girdle

Sternum

Poorly developed cartilaginous shield that is a symmetrical and lacks rib attachments (Zangerl. 1945; Al-Nassar, 1976; Gans, 1978). (Fig. 8.2a)

1, 2 - Interclavicle and clavicle

Absent (Cope, 1892; Camp, 1923 and Romer, 1956) except *Bipes* (Zangerl, 1945; Gans, 1978; Estes et al., 1988).

3- Scapulocoracoid and suprascapula

The scapulocoracoid is a small narrow elongated bone that lies lateral to the sternum along the anterior vertebrae (4~8 vertebrae). The distal end of the scapulocoracoid has a minute cartilaginous dorsal extension equivalent to the suprascapula (Fig. 8.2a). Gans (1960), described the scapulocoracoid as a bony appendage that was rod-shaped and divided into unequal portions.

In *Diplometopon*, the fore and hind limbs are absent, this is reflected in the vestigial structures of the sternum, pectoral and pelvic girdles (Bellairs, 1969; Al-Nassar, 1976). In *Bipes*, the elements of the pectoral girdle are well-developed (fused sternum, scapulocoracoid, cartilagenous suprascapula and vestigial clavicle) with retention of the front limbs (Zangerl, 1945). In *Blanus* the pectoral girdle is well-developed but there is no trace of limbs, while in all amphisbaenids, the distal end of the fore-limb is greatly reduced.

Muscles of *Diplometopon zarudnyi*

(Plate 8.3 - 8.4)

Superficial muscles

1- Depressor mandibulae

A short thin muscle bundle that originates posteriorly from the anterolateral margin of the oto-occipital (exoccipital), and inserts on the retroarticular process. The muscle attaches deep to the longissimus capitis 1 lateralis insertion.

2- Cervicomandibularis

The muscle runs anteriorly from its origin on the muscle fascia of the longissimus dorsi (superficial to the anterior cervical vertebrae) as an >

shape. The muscle has a broad insertion on the mandible (dentary) (plate 8.3a) and on the dorsolateral side of the parietal (anterior to the splenius capitis insertion) (plate 8.3b). Camp (1923), related powerful depressor and lateral adductor muscles of the head to stronger burrowers.

3, 4 - Trapezius and latissimus dorsi

Absent.

Intermediate muscles

1- Episternocleidomastoid

The muscle originates from the anterolateral edge of the small, cartilaginous sternum (vestigial pectoral girdle) (Fig. 8.2a). It inserts on the ventrolateral side of the otic capsule (plate 8.4a) (between longissimus capitis 1 lateralis and longissimus capitis 2 insertion).

2, 3, 4 - Levator scapula dorsalis/ventralis, clavicle dorsalis and ribs to suprascapula/ scapula muscle slips

Absent.

Deep muscles

1- Obliquus capitis

Originates from 2nd-5th neural spines, and extends anteriorly as one layer to insert on the paroccipital process.

2- Rectus capitis

Originates from the atlas and axis neural spines, and extends anteriorly to insert on the paroccipital process (dorsal to the obliquus capitis).

3- Splenius capitis externus and internus

Originates superficial to the 19th neural spine and muscle fascia, and extends anteriorly as one bundle until the 8th vertebrae where it is divided into two bundles (plate 8.3b) (externus and internus) which extend anteriorly to insert on the mid-anterodorsal edge of the parietal (superficial and deep insertion) (plate 8.3b).

4- Spinalis capitis and cervicus and spinalis/semispinalis complex):

Not investigated during dissection.

5- Longissimus muscles

a) Longissimus capitis 1 (medialis and lateralis)

The medialis branches superficial to the anterior cervical vertebrae and inserts as a tendinous bundle on the posterodorsal side of the parietal (lateral to the splenius capitis insertion) (plate 8.3c). The lateralis branches from the longissimus dorsi, and inserts on the ventrolateral side of the otic capsule (anterior to the episternocleidomastoid insertion).

b) Longissimus capitis 2

Branches anteriorly from the longissimus dorsi, and inserts anteriorly on the lateral and ventral edges of the paroccipital process (in an L-shape).

c) Longissimus capitis 3

Absent.

d) Longissimus capitis 4

Branches laterally beside the anterior cervical vertebrae and inserts ventrally on the ventrolateral edge of lower jaw (dentary).

e) Longissimus cervicus

See chapter 1.

f) Longissimus capitis minor

Absent.

Iliocostalis muscles

a, b) Iliocostalis major and cervicus

See chapter 1.

Longus muscles

a) Longus colli

Originates from the posterior edge of the 21st centrum (plate 8.2c), and extends anteriorly as a single thick bundle taking slips from the intercentral apices and lateral sides of the centra (Fig. 8.2c).

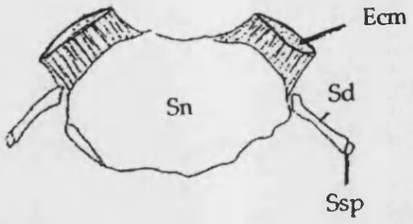


Fig. (8.2a) Ventral view of the pectoral girdle & sternum (Sn) showing the origin of episternocleidomastoid (Ecm) from sternum, also the scapulocoracoid (Sd) and the suprascapula (Ssp) in *D. zarudnyi*. Scale bar = 1 mm.

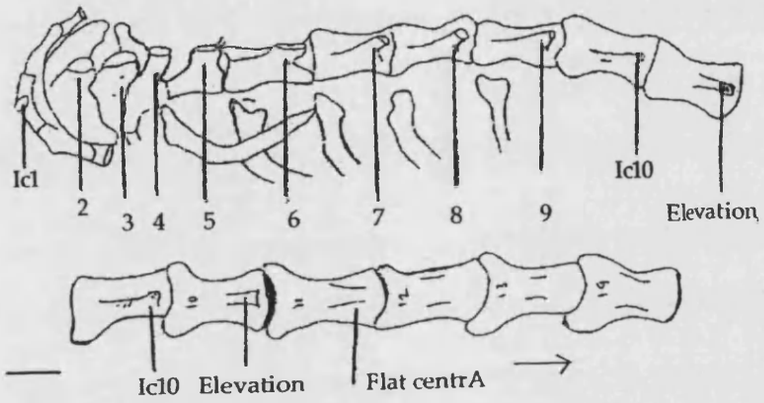


Fig. (8.2b) Left ventral view of the cervical & dorsal vertebrae in *D. zarudnyi*, with 10 keeled intercentra and small elevation on the 11th centrum, smooth dorsal centra and intercentra are fused to the preceding centrum . Scale bar = 1mm.

Fig. (8.2c) Ventral view of the vertebral column showing the origin of longus colli (Lci) from 21st centrum in *D. zarudnyi*. Scale bar = 1 mm.

The muscle finally inserts on the basal tubera and the ventral side of the oto-occipital (wide).

b) Longus cervicus (reduced)

Originates from the 7th intercentrum (vertebra 6) as a thin tendon, and extends anteriorly taking slips from intercentra and centra (plate 8.4c). The tendon inserts on the second intercentrum base (> shaped tendon).

3- First intercentral muscle slip to basioccipital

The first intercentrum gives origin to one muscle slip that ends on the middle region of the basioccipital beside longus colli insertion (plate 8.4c).

4- Posterior intercentral muscle slips to oto-occipital

These thick muscle slips originate from the apices of the 2nd-10th intercentra (vertebra 2-9) (plate 8.4b). They insert on the ventrolateral margin of the oto-occipital close to lateral part of the long narrow crista tuberalis and at the same level as the first intercentral muscle insertion.

Very deep muscles

1- 2nd-5th intercentral muscles to rib ligaments

After removing the longus cervicus, oblique muscle slips appear running from the 2nd intercentrum to the 1st rib, from the 3rd intercentrum to the 2nd rib, and from the 4th and 5th intercentra to the 3rd rib.

2- Deep intercentra short muscles to rib processes

Very deep short muscle slips that connect the bases of the intercentra to the small anteroventral processes of the costal heads (plate 8.4d). The first slip runs between the 4th intercentrum and the 1st rib; the second slip runs between the 5th intercentrum and the 2nd rib ... etc. The muscle slips continue back along the vertebral column.

Special craniocervical anatomical features in *Diplometopon zarudnyi*

Osteology

Skull

1- The parietal is long with deep ventral flanges. It is fused to the otic capsule posteriorly.

2-The squamosal is absent.

3- The supratemporal is very small and located between the otic capsule and quadrate.

4- The quadrate is triangular and does not contact the parietal.

Presacral vertebral column

1- The cervical region is not distinct from the trunk region.

2- The neural arches of posterior neural spines are absent and the neural arches are wide and flattened.

3- Prezygapophyseal processes are present and bear a keeled zygapophyseal processes which increases in size posteriorly (where longissimus dorsi muscle slips attach).

Ribs

1- The ribs does not attach to the reduced sternum .

2- The rib head bears a pseudotuberculum with a long narrow posterodorsal process and a small wide anteroventral process.

Pectoral girdle

It is vestigial. The sternum is reduced and is located anteriorly between vertebrae 4-8. The interclavicle and clavicle are absent, while the scapulocoracoid is narrow and short, and possesses a very tiny suprascapula.

Mylogy

Superficial muscles

1- The depressor mandibulae is very short and originates from the exoccipital part of the oto-occipital.

2- The cervicomandibularis originates from muscle fascia and inserts on the parietal and the mandible.

3- The trapezius and latissimus dorsi are absent.

Intermediate muscles

1- The episternocleidomastoid originates from the sternum and inserts on the otic capsule.

2- The levator scapula dorsalis/ventralis, clavicle dorsalis and ribs to suprascapula/scapula muscle slips are absent.

Deep muscles

1- The splenius capitis originates above vertebra 19, and extends anteriorly to divide above vertebra 8 into externus and internus bundles which continue forward to insert on the parietal.

2- The longissimus capitis 1 divided during insertion into two bundles, the medialis and lateralis. The latter inserts on the otic capsule, while the former inserts on the anterodorsal side of the parietal.

3- Longissimus capitis 2 inserts on the paroccipital process.

4- Longissimus capitis 4 inserts on the ventrolateral side of the mandible.

5- Longissimus capitis minor is absent.

6- The longus colli originates from the 21st centrum, and takes slips from the centra and intercentra, to insert on the basioccipital and oto-occipital.

7- The longus cervicus is reduced (one long tendon), and originates from 7th intercentrum of vertebra 6 to insert on the axis first intercentrum.

8- The posterior intercentral (2nd-9th) muscle slips insert on the long cristae tuberalis of the oto-occipital at the same level as first intercentrum muscle insertion.

Very deep muscles

1- Deep oblique intercentral slips to rib ligaments are present anteriorly.

2- Deep short intercentral muscle slips to adjacent ribs are present, so that the rib heads have a long dorsoposterior process and a wide short anteroventral process. The dorsal rib processes are connected to the centra laterally by short oblique muscles, while the ventral rib processes are connected to the intercentral bases ventrally by short oblique muscles. Both features run along the vertebral column.

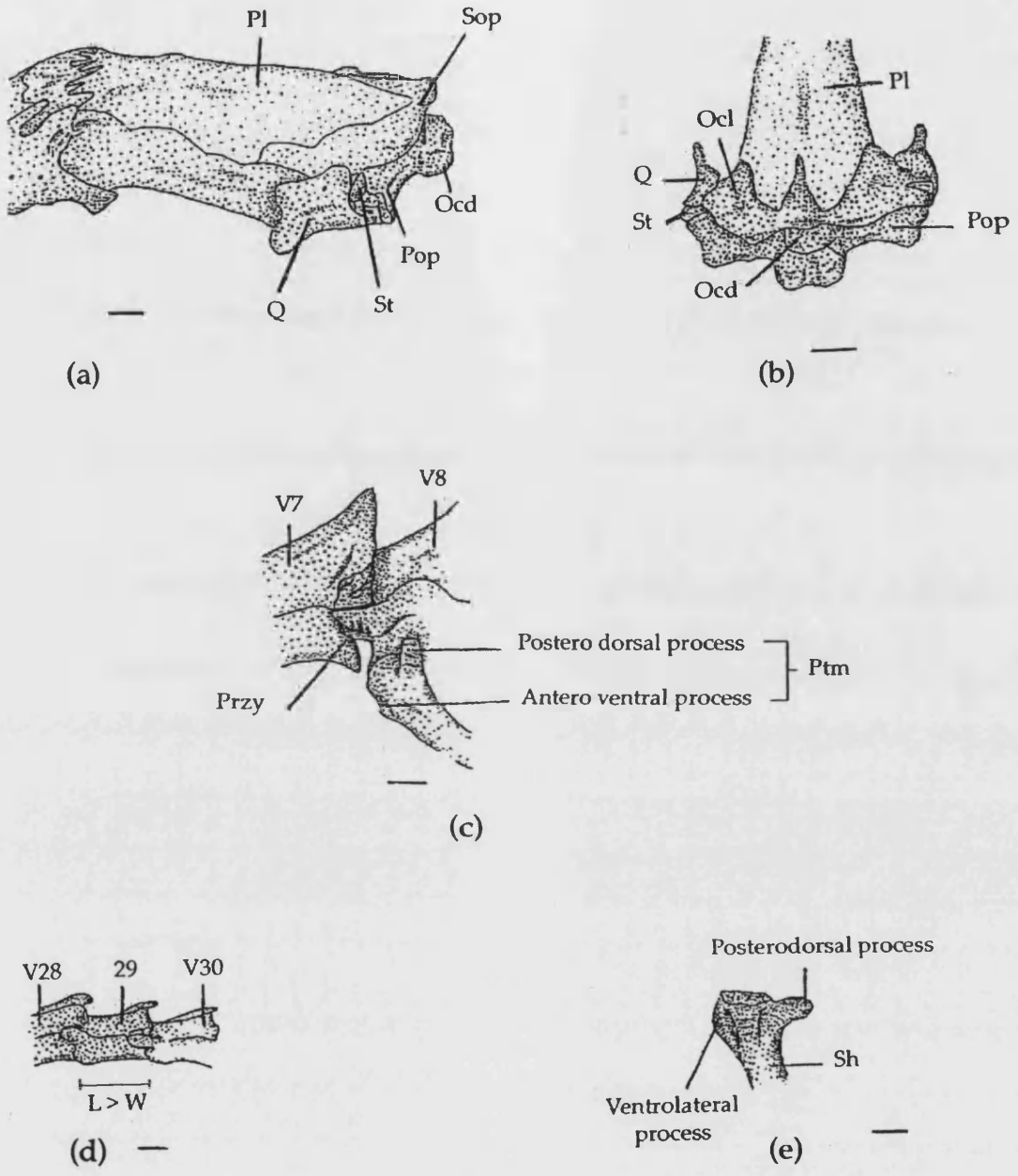


Plate (8.1) *Trogonophis wiegmanni,* a) left lateral view of the skull showing the elongated parietal, supraoccipital (Sop), supratemporal (St) and square quadrate (Q); b) posterodorsal view of the skull showing the non-smooth posterodorsal margin of the parietal which is fused to the supraoccipital and the paroccipital process; c) left lateral view of vertebrae 7 and 8 showing the articulation between vertebra and the prezygapophyseal process (Przy), also the rib pseudotuberculum (Ptm); d) left lateral view of posterior vertebrae where spines are nearly absent (flat) in the trunk region; e) anterior view of rib head with dorsal process and ventral crest = pseudotuberculum (Ptm). Scale bar = 1 mm.

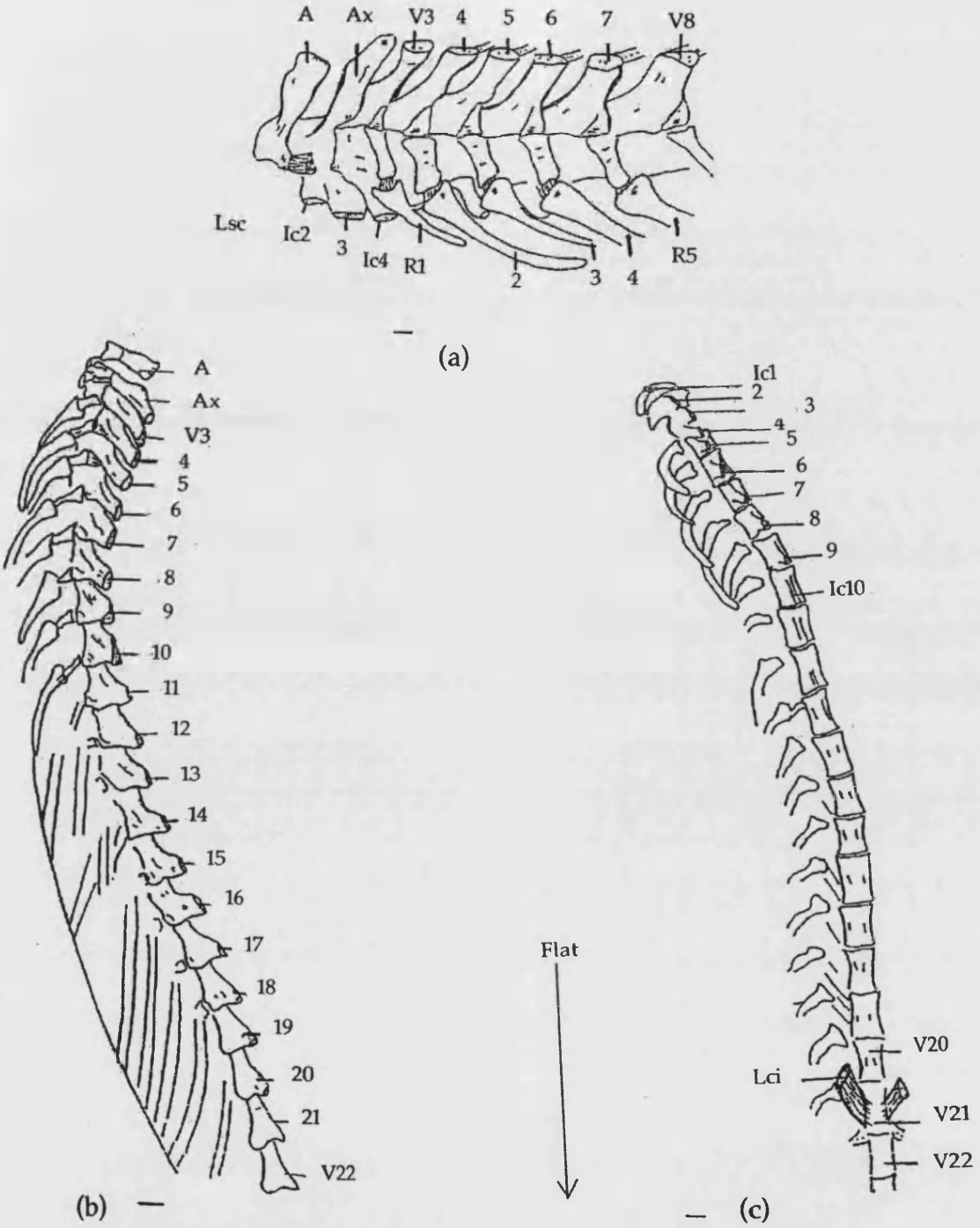


Plate (8.2) *Diplometopon zarudnyi*, a) left lateral view of the cervical vertebrae with a short axis spine, the first rib articulates with V4; b) right dorsolateral view of the anterior and posterior vertebrae showing neural spines which are distinctively high anteriorly and become flat posteriorly; c) left ventrolateral view of the anterior and posterior vertebrae showing 9 keeled intercentra and a small elevation (10th intercentrum), after which the centra became elongated and wide, longus colli (Lci) beginning on vertebra 21. Scale bar = 1 mm.

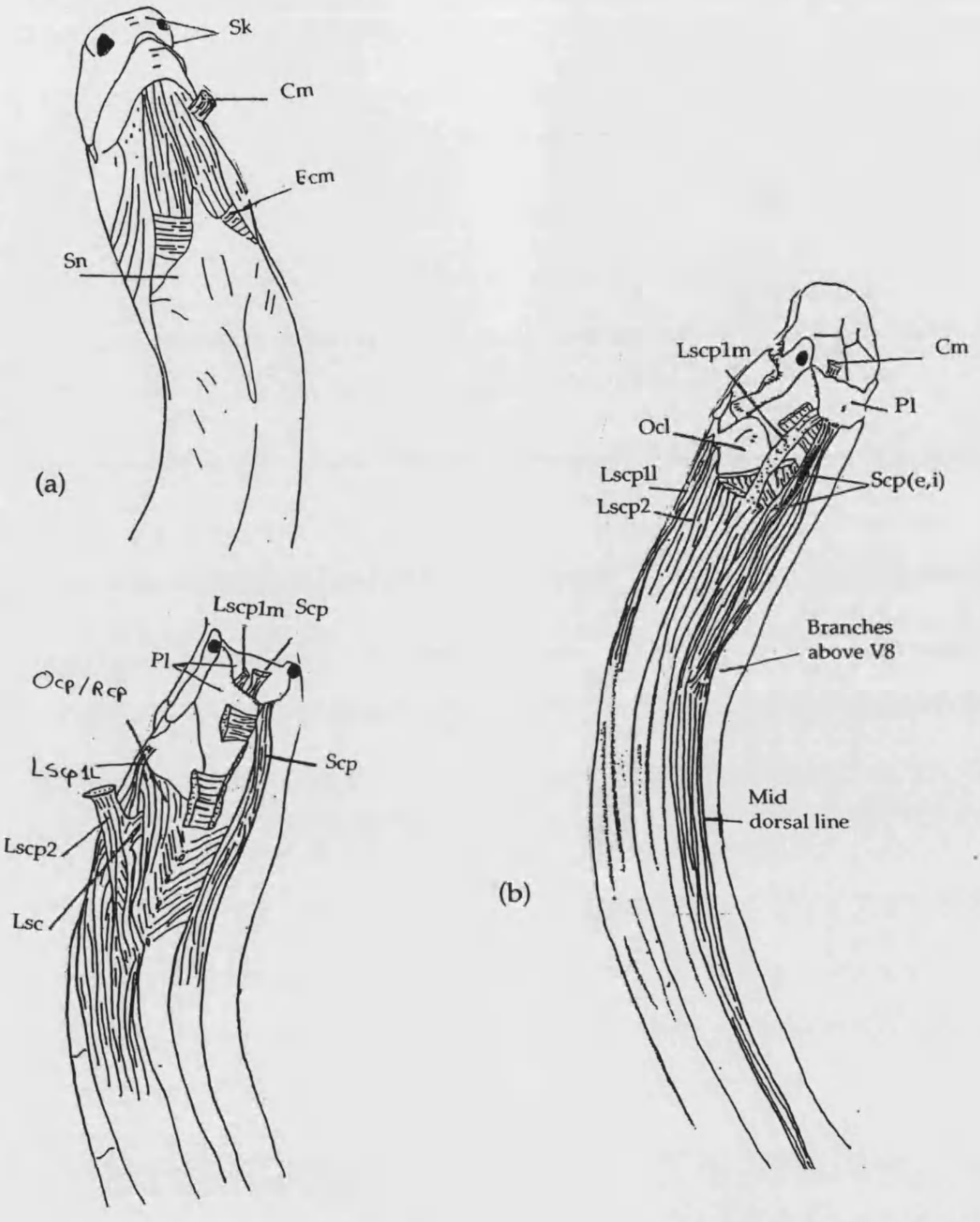
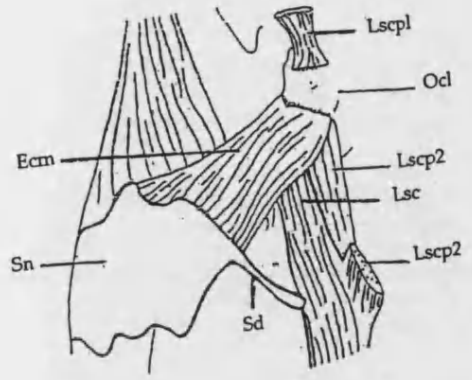
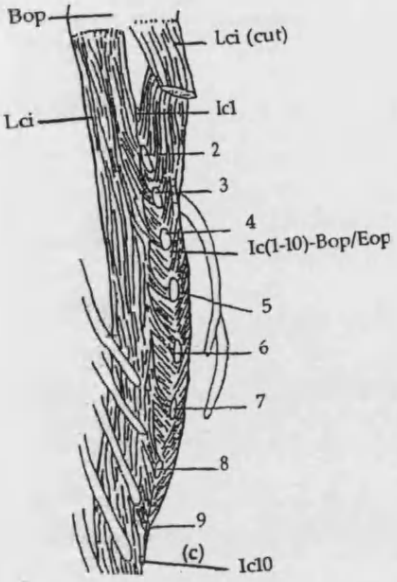


Plate (8.3) *Diplometopon zarudnyi*, a) ventral view of the craniocervical region with sternum (Sn) showing origin of episternocleidomastoid (Ecm), also the insertion of cervicomandibularis (Cm) on the mandible; b) dorsolateral view of the craniocervical region with longissimus capitis 1 (Lscp1) (Lscp1l, Lscp1m) and splenius capitis (Scpe,i) branches inserting on the parietal; c) dorsolateral view of the craniocervical region with longissimus capitis 2 (Lscp2) (cut) and longissimus cervicus (Lsc) extending deep and



(a)



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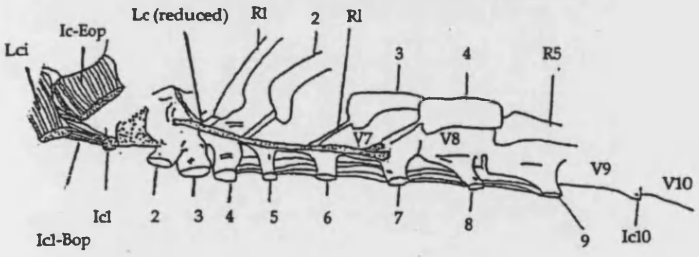

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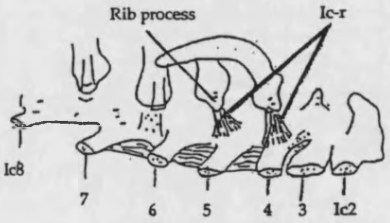


(d)

Plate (8.4) *Diplometopon zarudnyi*, a) ventrolateral view of the sternum (Sn) where episternocleidomastoid (Ecm) originates, and insertion on the otic capsule (Ocl), longissimus cervicus (Lsc) inserts on the atlas posterior process; b) ventral view of anterior vertebrae showing the longus colli (Lci) (cut) and intercentral muscle slips to skull (10 slips) (Ic[1-10]-Bop/Eop); c) left ventrolateral view of the craniocervical region showing the tendinous longus cervicus (Lc) origin and insertion; d) right ventrolateral view of the anterior vertebrae showing the short muscle slips between intercentra and rib heads (Ic-r). Scale bar = 1 mm.

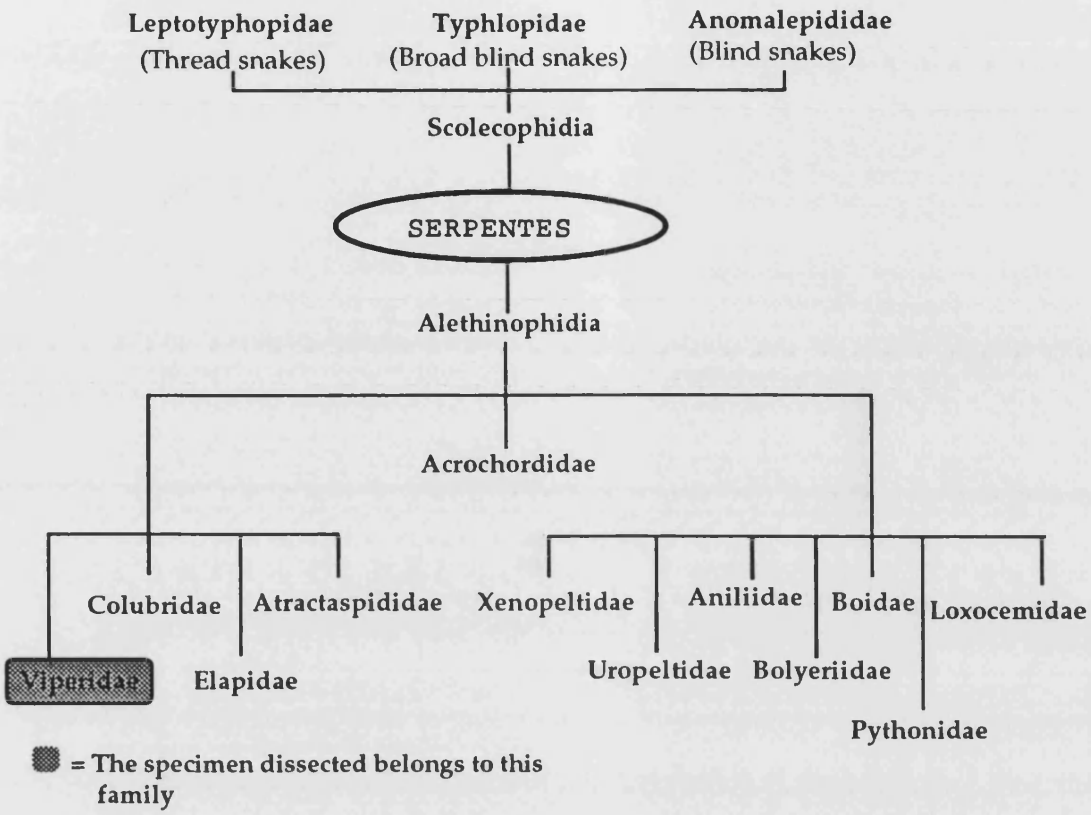
CHAPTER (9)

SERPENTES

Snakes are limbless squamates which show evolutionary tendencies toward lengthening the body and limb loss, possible as a result of a burrowing stage in their early history (as suggested by the structure of the reduced eye, Walls, 1942, and ears) or instead because of an aquatic swimming phase (Caldwell and Lee, 1997). Snakes share limblessness with several groups of lizards, but their exact relationship to other squamate groups remains uncertain, although snakes are certainly scleroglossans and almost certainly anguimorphs (Young, 1981; Zug, 1993).

The earliest fossils of snakes are known from Cretaceous deposits. Snakes have diversified during recent geological history, and now successfully occupy most parts of the planet except the Arctic, Antarctica, Ireland, New Zealand and some small oceanic islands. Serpentes includes 18 families, 450 genera and about 2,700 species. Length ranges from 150mm (e.g. thread snakes and blind worm-snakes) to 10m (e.g, the Anaconda - *Eunectes murinus*) (Halliday and Adler, 1986; Shine, 1992).

The Scolecophidia are small burrowing snakes that have smooth overlapping scales across their entire cylindrical bodies; their eyes and dentition are reduced; they lack vertebral neural spines and intercentra; and retain a trace of a pelvic girdle. The Alethinophidia are a diverse group that include some burrowers (small to moderate size) and the boas and pythons (mostly not burrowers). More advanced alethinophidian snakes possess large eyes (e.g. Colubridae) and a head broader than the neck (e.g. Viperidae). The acrochordids (elephant-trunk snakes) have baggy loose skin that enables them to swim more efficiently (Webb, et al., 1978; Zug, 1999).



(9.1) Diagrammatic representation of snake relationships (Webb, et al., 1978; Zug, 1993).

Snake locomotion: The length of the vertebral column (=400 vertebrae) and the presence of the accessory articulation facets (zygosphene and zygantrum) assists in flexibility while providing stability. Snakes move using several distinctive methods:

a) Serpentine locomotion (horizontal or lateral undulation), the most common movement in reptiles especially snakes. It involves the passage of a number of waves that originate from the head and run along the body. If pressed against a resistance (obstacles, stones and vegetation) the force of the muscular contractions in the trunk region alter the curvature and push the animal forward (Gans, 1973b - e.g. burrowing uropeltids).

b) Rectilinear creeping ("caterpillar principle"), most common in terrestrial snakes. This method depends on muscle contractions that act on the skin of the belly and the ventral scales. The resistance of the

ground against some irregularities on the scale draws the snake's body forward in a straight line (Gans, 1973b).

c) Concertina locomotion, where the anterior body is pushed forward in a horizontal loop until it finds a support, then the body follows (Gans, 1973b).

d)"Side winding" or slide-pushing, is common in snakes that inhabit sandy deserts and completely smooth substrates. It is a lateral rolling spiral where the snake does not rest on the substratum completely, and moves sideways.

e) Gliding, a few colubrid snakes launch themselves between trees by flattening their bodies during flight and landing (Mertens, 1960; Parker, 1977; Duellman and Heatwole, 1992; Shine, 1992).

Anatomy of the neck region in an advanced snake

Family : Viperidae

Trimeresurus wagleri (Dissected)

Trimeresurus albolabris (*Lachesis gramineus*) (Skeleton)

One snake was dissected simply for comparison with other limbless and limbed squamates. The taxon dissected was an advanced snake of the family Viperidae.

Previous work:

Sood, 1948; Mosauer, 1935; Bellairs and Underwood, 1951; Romer, 1956; Underwood, 1957; Gans, 1962, 1973a, b; Auffenberg, 1962; Hoffstetter and Gayrard, 1964; Gasc, 1967, 1981; Bellairs, 1969; Hoffstetter and Gasc, 1969; Parker, 1977; Estes et al., 1988.

Osteology of *Trimeresurus wagleri*

(Plate 9.1)

Skull

1- Parietal

The midposterolateral margin is smooth (where splenius capitis inserts), and the posterodorsal processes are absent (plate 9.2d).

2- Squamosal

Absent (Estes et al., 1988).

3- Supratemporal

This is a small bone which is situated between the parietal dorsally and the quadrate ventrally (plate 9.2d).

4- Quadrate

This is elongated highly movable bone (plate 9.2b) (where depressor mandibulae internus originates) which is free from the pterygoid. The posterolateral margin is straight. In uropeltids, the quadrate is relatively small (Gans, 1973a).

5- Retroarticular process

The process is reduced, with a pointed posterior end (where depressor mandibulae inserts).

6- Supraoccipital

Superiorly, it has a rounded midline ridge (where rectus capitis inserts). Dorsally the supraoccipital is fused with the parietal.

7- Oto-occipital

The paroccipital process is wide. The ventrolateral margin of the oto-occipital has a long thick crista tuberalis (where hypapophyses to oto-occipital and basioccipital muscle slips insert).

8- Paroccipital epiphysis

Absent.

9- Basioccipital

The basal tubera are not distinguished as in other squamates, but, two tiny posterior processes are located in the centre of the basioccipital (where longus colli inserts).

Precloacal vertebral column

1- Atlas

The posterior process is long and pointed. The transverse process is posteriorly long, while the hypapophysis is deeply keeled (plate 9.1b).

2- Axis

The postzygapophyses are horizontal and possess posterior process (plate 9.1a). The transverse processes project strongly posteriorly. Ventrally the centrum has fused second and third hypapophyses (single blade) which are smooth.

3- The anterior and posterior vertebrae (vertebral column)

The cervical region is not differentiated from the dorsal region as the pectoral girdle is absent and the hypapophyses continue posteriorly along the entire trunk region (Bellairs and Underwood, 1951) (plate .1c, d). Generally, the same authors with Romer (1956), Hoffestetter and Gasc (1969) and Bellairs (1969) recorded the number of vertebrae as ranging from 140-400. The neural spine width is greater than the length and their anterior margins are smooth and curved, while the posterior margins are straight and possess a convex sharp edge above the postzygapophysis (where the wide interneural arch/spine muscle slips attach) (plate 9.1f, g). In most snakes the neural spines are highly developed with a vertical orientation along the whole vertebral column, but in burrowers the spines are reduced (Hoffstetter and Gayrard, 1964; Hoffstetter and Gasc, 1969). The neural arches bear paired zygosphenes that articulate with the posterior zygantral fossa of the preceding vertebrae (Gans, 1962; Estes et al, 1988) (plate 9.1f). These zygosphenic articulations are absent in limbless lizards (e.g. anguids) (Romer, 1956; Gasc, 1967, 1969; Parker, 1977). The postzygapophyses are horizontal and possess a posterodorsal process (where spinalis/semispinalis complex attaches). Auffenberg (1962), described the presence of a projection behind the postzygapophyses as the epizygapophysial spine. The prezygapophyses

bear thick ventral prezygapophyseal processes (where deep ventral muscles attach) (Mosauer, 1935; Sood, 1948).

Ventrally, the centra lack a mid-ventral keel and the hypapophyses are smooth and fused to the centra in front (Estes et al, 1988). The hypapophyses continue along the entire vertebral column (Bellairs and Underwood, 1951), while internal to the rib facet, there is parapophysial anterior process (where the hypapophyses-parapophysial muscles attach).

Ribs

The first rib starts on C4 (plate 9.1e), and all ribs are connected to the adjacent centra by a ligament. The first and second ribs are shorter than the posterior ribs. All ribs have pseudotuberculum (narrow posterodorsal processes and wide anteroventral processes) which have symmetrical shapes. The posterior ribs are uniform (smooth and rounded) and lack cartilage ends.

Pectoral girdle

1- Sternum

Absent.

2,3,4,5- Clavicle, interclavicle, scapulocoracoid and suprascapula

Absent (Romer, 1956; Underwood, 1957; Bellairs and Underwood, 1951; Bellairs, 1969). The pelvic girdle is usually absent, but sometimes it is vestigial with a reduced hind limb (e.g. femur) present (e.g., Leptotyphlopidae, Aniliinae and some Boidae [Romer, 1956]). However, in *Trimeresurus* the pelvic girdle area was not investigated.

Muscles of *Trimeresurus wagleri*

(Plate 9.2 - 9.3 - 9.4)

Superficial muscles

1- Depressor mandibulae internus and externus

3- Splenius capitis

Originates from the neural spines of the 2nd-8th vertebrae, and extends anteriorly as one layer to insert on the mid-posterodorsal edge of the parietal (plate 9.2d).

4- Spinalis muscles

a) Spinalis capitis

Absent.

b,c) Spinalis/semispinalis cervicus and spinalis/semispinalis complex

Not investigated during dissection.

5- Longissimus muscles

a) Longissimus capitis 1

Branches from the longissimus dorsi, and inserts on the mid-posterodorsal side of the parietal (lateral to the splenius capitis insertion).

b) Longissimus capitis 2

Branches from longissimus dorsi and inserts on the dorsolateral edge of the oto-occipital towards the supraoccipital and lateral to longissimus capitis 1 (plate 9.3a).

c) Longissimus capitis 3

Absent.

d) Longissimus capitis 4

Branches laterally deep to the longissimus dorsi, and inserts on the ventrolateral tip of the oto-occipital close to the basioccipital and dorsally to the posterior hypapophyses muscles to skull (plate 9.3b).

e) Longissimus cervicus

See chapter 1.

f) Longissimus capitis minor

Absent.

6- Iliocostalis muscles

a,b) Iliocostalis major and cervicus

See chapter 1.

7- Longus muscles

a) Longus colli

Originates from the 10th hypapophysis (9th vertebra) (plate 9.3c, 9.4a) and extends anteriorly as a single long muscle with slips from the hypapophyses and centra. The muscle inserts (muscle fibers) on the central basal tubera (plate 9.3c).

b) Longus cervicus

Absent.

8- First hypapophysis to basioccipital muscle

Originates from the first hypapophysis and inserts on the basioccipital as a single layer deep to the longus colli and other posterior hypapophyses muscles.

9- Posterior hypapophyses to basioccipital/oto-occipital muscle

Originates from the apices of 2nd-6th hypapophyses (begins on vertebra 5), and extends anteriorly to end on the basioccipital (near the central basal tubera and oto-occipital) (plate 9.4b). Ventrally, the muscles insert broadly deep to longus colli, and superficial and lateral to the first hypapophysis muscle insertion.

Very deep muscles

1- Deep oblique hypapophyses muscle slips to rib distal ends

Very specialised oblique muscle slips that originate from the lateral side of the hypapophyseal apices and extend anteriorly to end on the distal ends of the short ribs (plate 9.4c). For example, the 10th hypapophysis muscle (where the first muscle slip originates) extends anteriorly to end on the distal side of the first rib, on vertebra 4 ... etc.

2- Deep ventral hypapophyses to parapophysial processes/rib ligaments muscle slips

These muscle slips run ventrally in a deep position along the vertebral column (deep to the posterior hypapophyses muscle slips to skull) as a tendinous bundle (from posterior apex of the hypapophyses), and as a muscle layer (from posterior edge of the hypapophyses) (plate 9.4d). Mosauer (1935) called them "transverso--hypapophyseus", while Gasc (1981) referred to them as "M. parapophysco-hypapophyseus", and reported their presence in the trunk. The muscles insert on the parapophysial processes and rib ligaments laterally. The most anterior muscle slip runs between the 3rd hypapophysis and the parapophysial processes of the 4th and 5th vertebrae. The parapophysial processes also have short thin muscles running between them.

Special anatomical features in *Trimeresurus wagleri*

Osteology

Skull

1- The posterolateral processes of the parietal are absent, and the parietal is fused to the oto-occipital bone.

2- The squamosal is absent.

3- The quadrate is an elongated, narrow, movable bone. It does not contact the parietal.

4- The basal tubera are central in position.

Precloacal vertebral column

1- The cervical region is not distinct from the trunk region.

2- The posterior neural spines have a convex sharp posterior edge (where the interneural arch/spine muscles attached).

3- The neural arch has accessory articulating facets on the posterior (zygosphene), and anterior (zygantrum) sides of the arch.

4- The prezygapophyses have prezygapophyseal processes (where longissimus dorsi muscle slips attach).

5- The hypapophyses continue along the entire vertebral column.

6- Ventrally, there are parapophysial processes below and posterior to the transverse processes (where hypapophyses to parapophyseal muscle slips attach).

Ribs

1- The ribs do not attach to the reduced sternum .

2- The ribs head bear pseudotubercula with long narrow posterodorsal processes and small wide anteroventral processes.

Pectoral girdle

Sternum, clavicle, interclavicle, scapula and suprascapula are absent.

Myology

Superficial muscles

1- The depressor mandibulae internus and externus originate from the muscle fascia of splenius capitis. The internus branch inserts on the quadrate, while the externus inserts on the quadrate and retroarticular process.

2- The trapezius and latissimus dorsi are absent.

3- Basioccipital and parietal to quadrate muscles are present.

Intermediate muscles

Absent.

Deep muscle

1- Longissimus capitis minor is absent.

2- The longus colli originates from the hypapophyses. It extends centrally to insert on the central basal tubera.

3- The longus cervicus is absent.

4- The posterior hypapophyses (2-6) muscle slips insert widely on the ventrolateral margin of the oto-occipital and basioccipital. The muscle slips insert partially superficial to the first hypapophysis muscle slip.

5- There are muscle slips running between the hypapophyses apices to rib distal ends; from the hypapophyses to parapophyseal processes and centra; and between adjacent parapophyses processes.

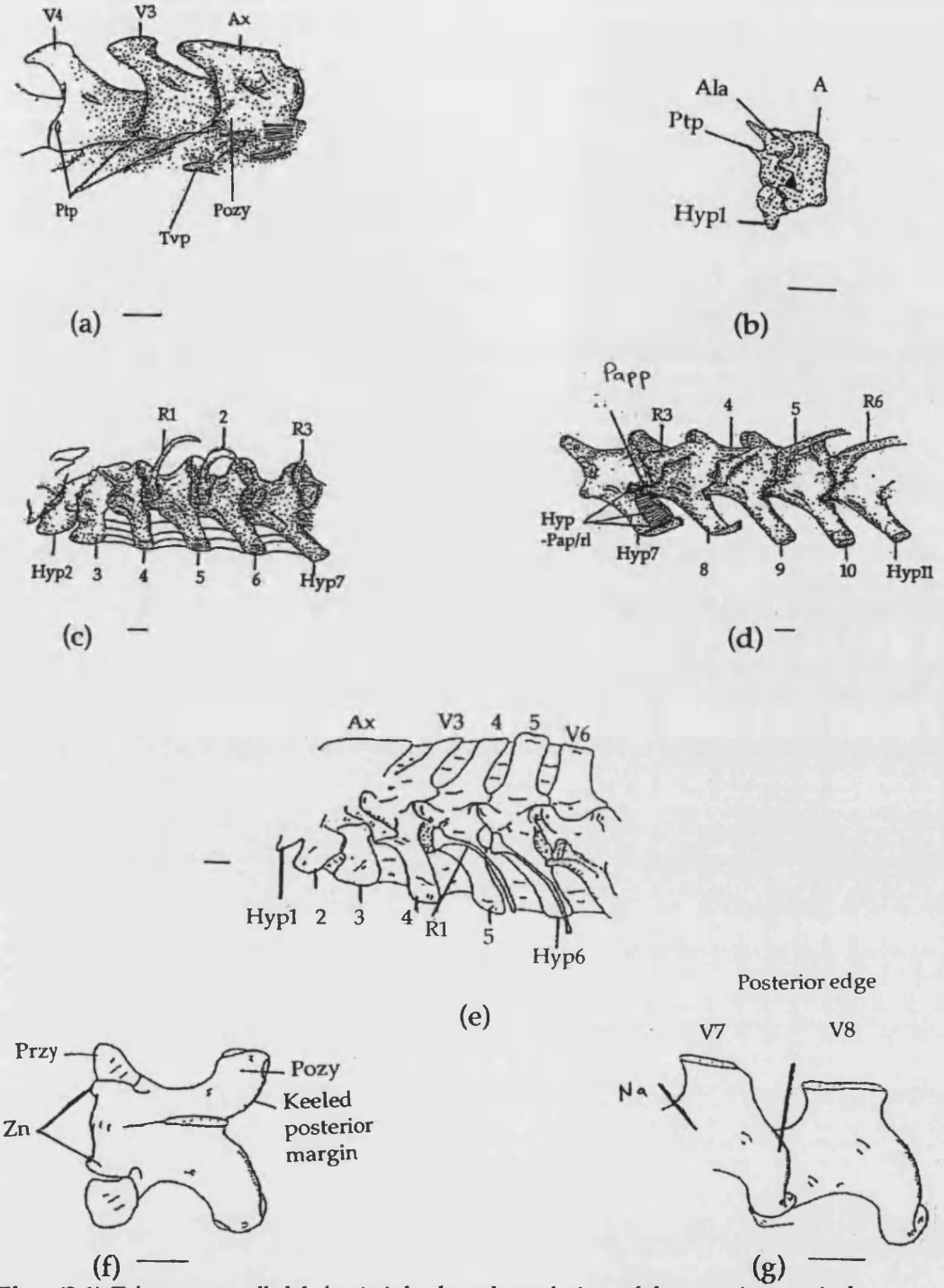


Plate (9.1) *Trimeresurus albolabris*, a) right dorsolateral view of the anterior cervical vertebrae showing the shape of the axis (Ax), 3rd and 4th vertebral spines, neural arches and postzygapophyses (Pozy) with posterior (Ptp); b) right lateral view of the atlas showing the atlantal arches (Ala), posterior processes (Ptp) and 1st hypapophysis (Hyp1); c) *T. albolabris*, left ventrolateral view of anterior keeled hypapophyses (1-7); d) *T. albolabris*, left ventrolateral view of keeled hypapophyses (7-11) with parapophyses process (Papp) ventral to the ribs (Hyp-Papp/ rl); e) *Trimeresurus wagleri*, left lateral view of anterior vertebrae (2-6) with deep keeled hypapophyses and narrow short ribs which start on vertebra 4; f) *Trimeresurus wagleri*, right dorsal view of an anterior vertebra with zygapophyses (including zygosphene - Zn); g) left dorsolateral view of vertebrae 7 and 8 showing the sharp edge along the posterior margin of the postzygapophyses (Pozy). Scale bar 1 = mm.

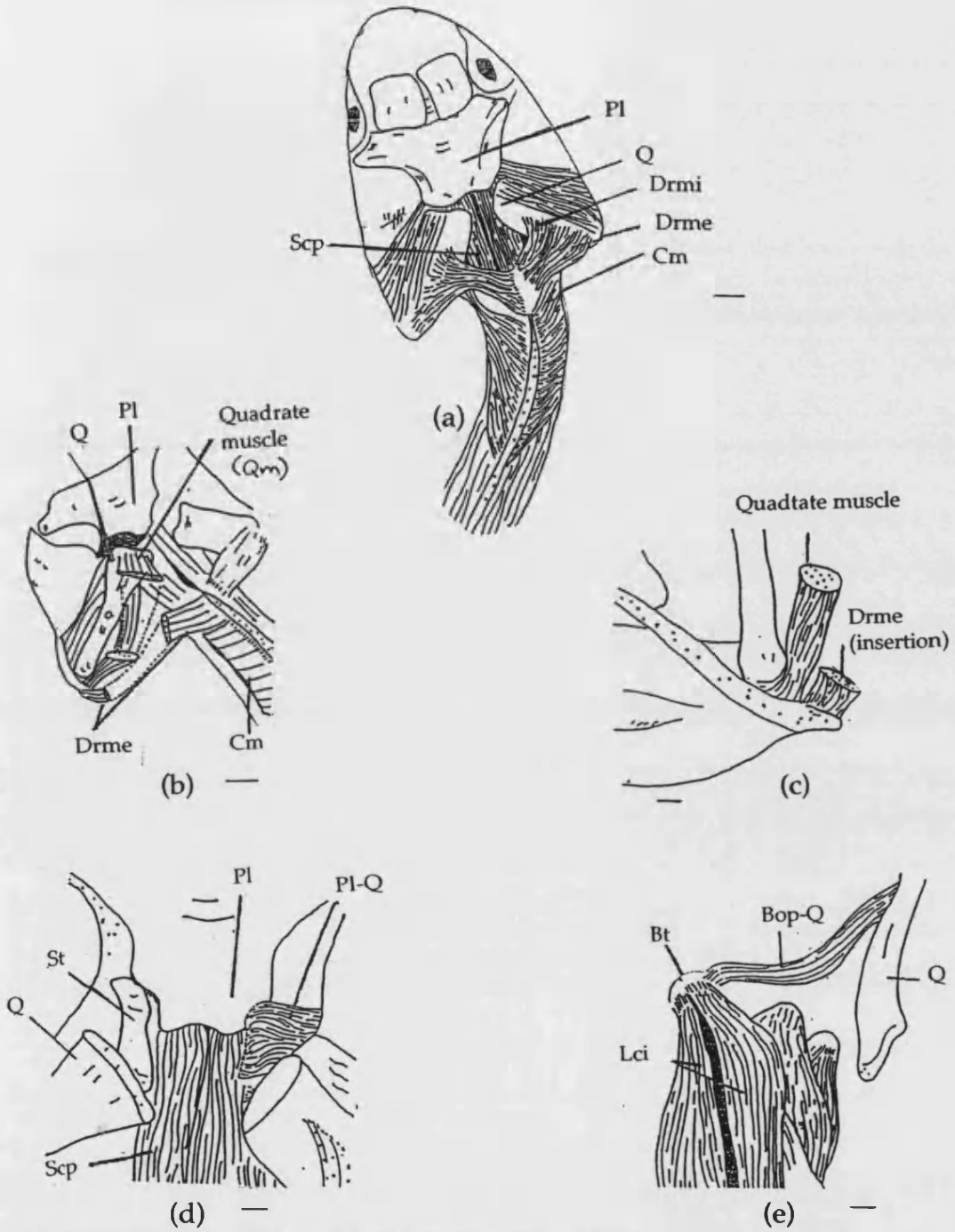


Plate (9.2) *Trimeresurus wagleri*, a) left dorsal view of the craniocervical region where cervicomandibularis (Cm) and depressor mandibulae (Drm) originate from muscle fascia; b) left dorsal view of the skull showing the depressor mandibulae (Drm) inserting on the retroarticular process (Rp), with an internus branch which originates from the quadrate (Qm); c) left posterolateral view of the lower jaw showing the insertion of depressor mandibulae and quadrate muscle (Qm) on the retroarticular process (Rp); d) dorsal view of the skull showing the parietal to quadrate (Pl-Q) muscle along the supratemporal (St); e) left ventrolateral view of the skull showing the basioccipital to quadrate muscle (Bop-Q). Scale bar = 1 mm.

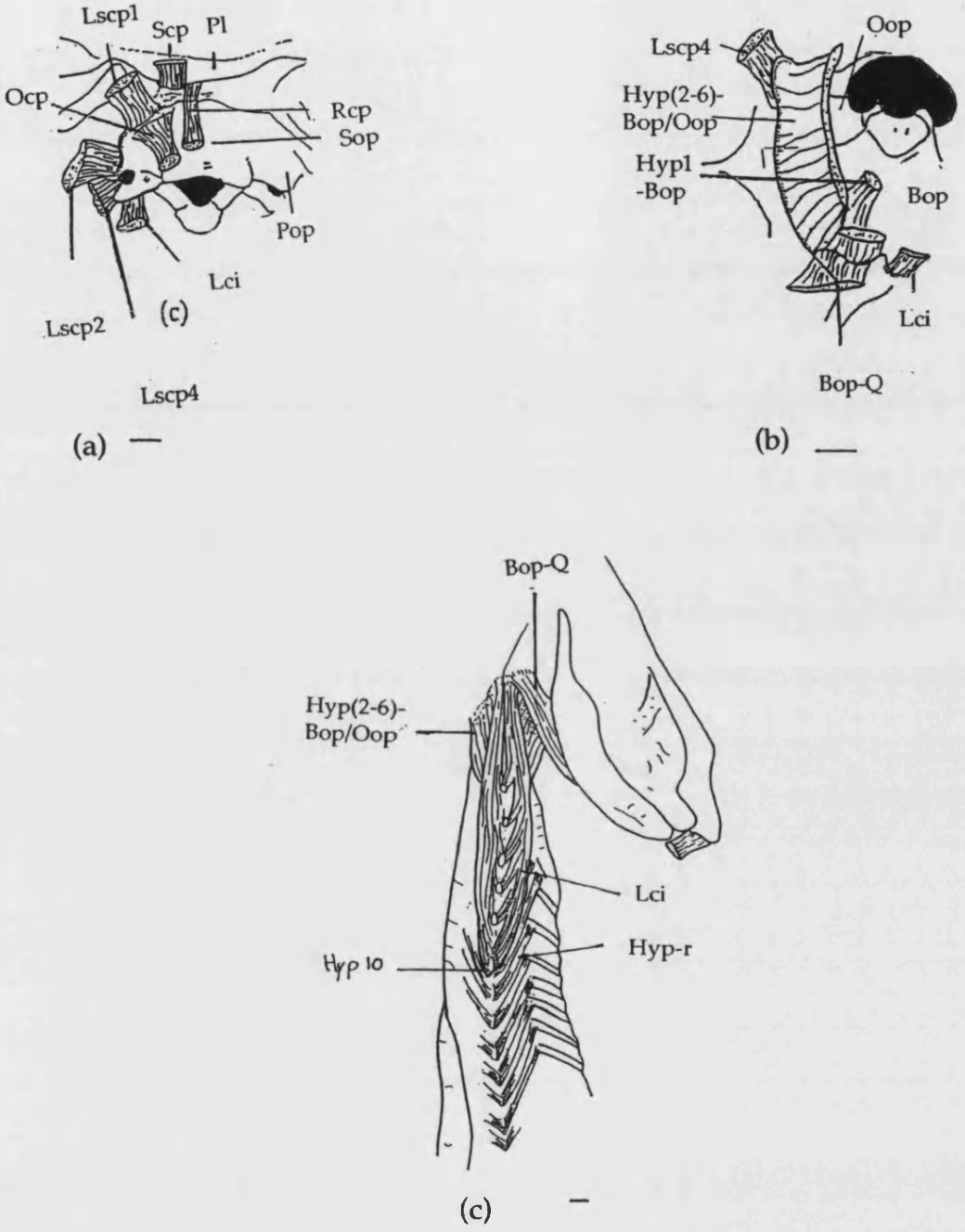


Plate (9.3) *Trimeresurus wagleri*, a) occipital view of the skull with deep muscle insertions; b) posteroventral side of the skull with a wide insertion of posterior hypapophyses muscle on basioccipital and oto-occipital (Hyp[2-6]-Bop/Oop), first hypapophysis muscle (Hyp1-Bop) inserts under the posterior hypapophyses muscles and longus colli (Lci); c) ventral view of the craniocervical region showing the start origin of longus colli (Hyp10) and its central insertion on the basioccipital, also the attachment of basioccipital to quadrate (Bop-Q) muscle ventral to longus colli (Lci);. Scale bar = 1 mm.

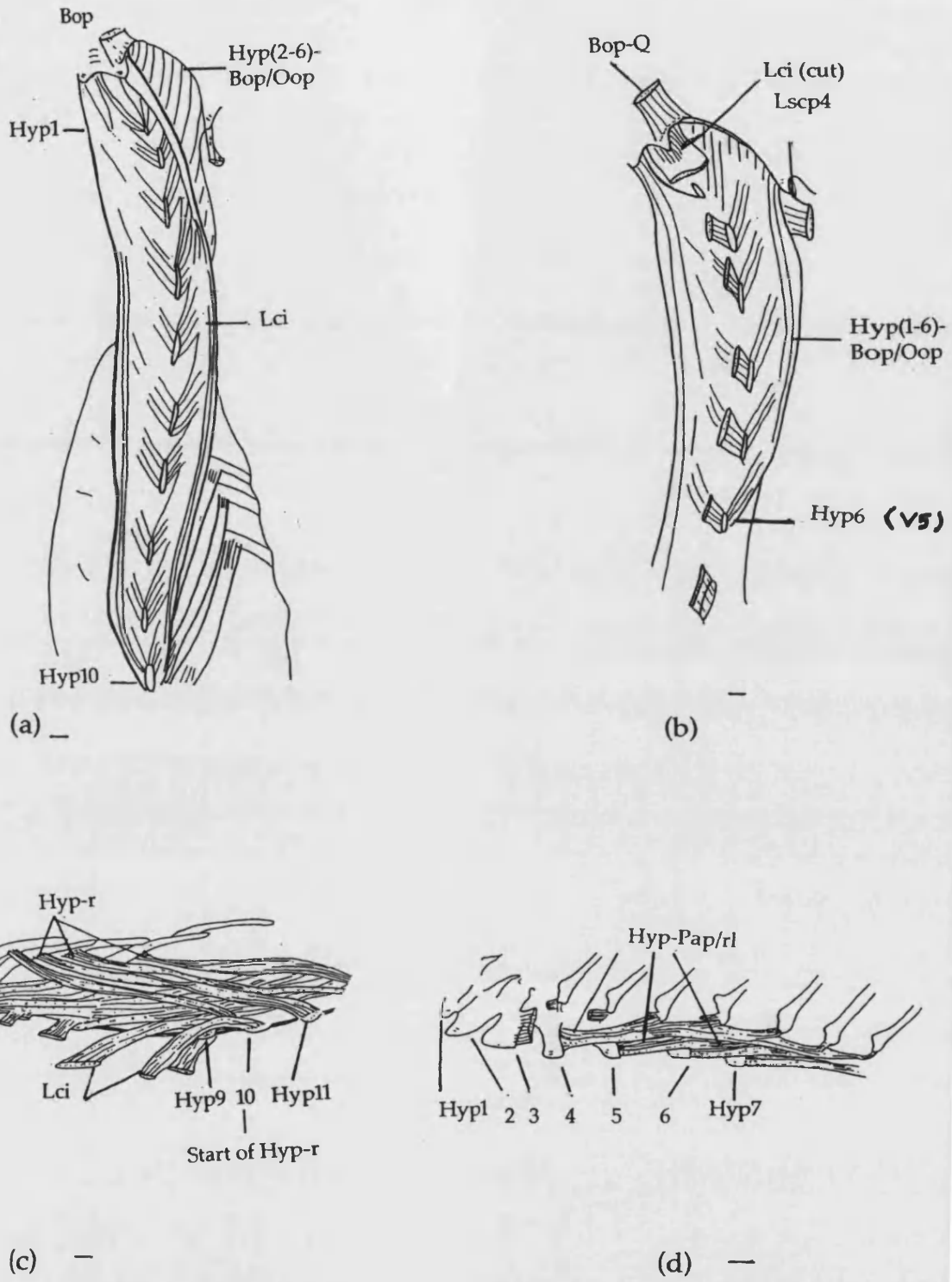


Plate (9.4) *Trimeresurus wagleri,* ventral view of the craniocervical region a-b, a) origin, extension and insertion of longus colli (Lci); b) hypapophyses muscle slips to basioccipital and oto-occipital (Hyp[1-6]-Bop/Oop). Left ventrolateral view of the anterior cervical vertebrae, c) posterior hypapophyses to rib shaft muscle slips (Hyp-r) which start on the 10th hypapophysis (Hyp10); d) very deep hypapophyses posterior margin to rib head and parapophyses muscle (Hyp-pap/rl). Scale bar = 1 mm.

III - DISCUSSION

CHAPTER (10)

A detailed review of the osteology and myology of the lepidosaurian cervical region has never previously been made. Studies of this kind have the potential to contribute to an understanding of relationships, as a basis for following the sequence of structural and functional changes that occurred during the evolution of living groups (Gans, 1966a, 1969b). Increasingly both osteological and, to a lesser degree, myological characters are being used for cladistic studies. There is a need for older characters to be scrutinised and new characters to be identified. Within the context of character analysis, but also for palaeontology, it is also important to understand the relationship between muscles and bone. This discussion is therefore in two parts:

STRUCTURAL ANALYSIS

1- Relationships between muscles and bones.

2- The occipital surface of the skull.

3- The ventral side of the cervical region.

4- The atlas-axis complex.

5- The pectoral girdle and sternum.

CHARACTER DISTRIBUTION AND PHYLOGENY

6- Intraspecific and interspecific variation.

7- Character distribution in the neck region of Squamata and *Sphenodon*, using *Caiman* as an outgroup.

STRUCTURAL ANALYSIS

1- Relationships between muscles and bones

The axial musculature is relatively diverse in lepidosaurs, and especially in Squamata as a result of locomotor adaptations (Gasc, 1981). However, muscle and bone are intimately associated. The function of the muscle is to produce force, which is applied to the skeletal elements. These muscle forces pull directly on their attachment area (Haskell et al., 1986) and produce characteristic features (e.g. tuberosities, rugosities), or cause bones to be loaded as levers with associated bending (Herring, 1993).
In the following section, features visible on the posterior surface of the skull, the cervical vertebrae, and the pectoral girdle of lepidosaurs were examined and related, where possible, to the associated muscles.

Skull

1) The development of the retroarticular process in relation to the depressor mandibulae

	Narrow origin of depressor mandibulae on the skull or muscle fascia	Wide origin of depressor mandibulae on the skull or muscle fascia
Well-developed retroarticular process	*Oplurus, Crotaphytus;* agamids gekkotans; *Caiman*	*Anolis richardii, Iguana;* scincomorphs; anguimorphs
Reduced retroarticular process	*Sphenodon;* chamaeleons *Diplometopon; Trimeresurus*	*Phrynosoma*

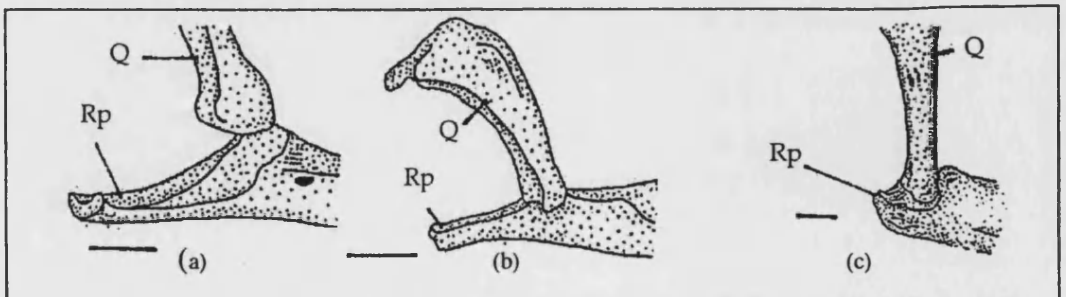


Fig. (10.1.1) Right lateral view of the skull showing the retroarticular process (Rp) and quadrate (Q) in a) *Diplodactylus* (gekkonid), b) *Tiliqua* (scincid), c) *Sphenodon*. Scale bar = 1 mm.

- Muscle related to that area:

  Depressor mandibulae internus and externus (origin).

- Muscle trace on the bone:

  The retroarticular process can be well developed, slightly developed or reduced. The depressor mandibulae inserts on the retroarticular process in all taxa. The size of the muscle at its dorsal origin (wide or narrow) does not appear to affect the shape and development of the process such that a long retroarticular process can occur with either a wide or narrow muscle insertion (e.g. agamids have a narrow muscle origin and Scincomorpha a wide origin, but both have a well-developed retroarticular process {Fig., 10.1.1b). In other taxa such as *Diplometopon, Trimeresurus, Sphenodon* and chamaeleons, the reduced process (plate 10.1.1c) (Camp, 1923; Romer, 1956; McDowell and Bogert, 1954; Rieppel, 1981) is combined with a narrow depressor mandibulae origin, but other factors (e.g. ear reduction) may also be involved.

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2) Presence or absence of the parietal posterolateral process

Present	*Sphenodon* (short); iguanids, agamids, gekkotans, scincomorphs; anguimorphs (long), *Diplometopon* (descending flanges).
Absent	*Caiman; Trimeresurus;* chamaeleons.

- Muscles related to this area:

  Depressor mandibulae internus (origin).

  Longissimus capitis 1 (insertion).

  Longissimus capitis 2 (sometimes - insertion).

  (but also jaw adductor muscles not examined)

- Muscle trace on the bone:

The presence of the posterior processes on the parietal is primitive for diapsid reptiles. If the posterolateral processes are absent, then the related muscles attach to the following:

	Caiman	*Trimeresurus*	Chamaeleons
Depressor Mandibulae	Quadrate + squamosal	Quadrate	Quadrate + squamosal or supratemporal
Longissimus capitis 1	Absent	Parietal dorsally	Supraoccipital
Longissimus capitis 2	Paroccipital process	Oto-occipital dorsally	Paroccipital process + squamosal or supratemporal

The shift of the depressor mandibulae origin to the quadrate in *Caiman* is not surprising, since the quadrate is fixed. Its origin from this bone in taxa with a highly mobile quadrate is less easy to explain, unless it has become involved in quadrate movement.

---

3) The shape of the mid-line ridge of the supraoccipital

Smooth	*Hemidactylus, Chondrodactylus ; Uromastyx*
Rounded	*Caiman; Ceratophora, Moloch, Draco, Calotes, Phrynocephalus, Agama, Pogona; Tarentola, Phelsuma, Gekko, Ptychozoon, Uroplatus, Eublepharis; Scincus, Tiliqua rugosas, Acanthodactylus; Varanus, Shinisaurus,* most anguids (e.g. *Diploglossus crusculus*); *Trimeresurus; Diplometopon.*
Sharp mid-line ridge	Iguanids; chamaeleons (with the sharp crista parietalis inferior), *Tiliqua nigrolutea,* cordylids, *Lacerta trilineata, Lacerta lepida,* teiids; *Heloderma; Diploglossus monotrofis.*
Crest	*Sphenodon; Diplodactylus.*

- Muscle related to this area

Axis to supraoccipital muscle (insertion).

Splenius capitis (insertion).

Rectus capitis (insertion).

- Traces of the muscle on the bone

Superiorly, the supraoccipital is either smooth, rounded, keeled or has a posterior crest. The rectus capitis always inserts on the supraoccipital but leaves only a smooth, rounded or sometimes weakly keeled mid-line ridge. In *Sphenodon*, the presence of the atlas to supraoccipital muscle results in the appearance of a short posterior crest on the supraoccipital. In Iguanidae*, the splenius capitis extends ventrally to insert on the mid-line ridge of the supraoccipital resulting in the appearance of a sharp keel, but other taxa with a sharp ridge do not show the same muscle arrangement and the explanation is clearly more complex. The character also shows interspecific variation (e.g. *Tiliqua* and *Diploglossus*).

---

4) A shallow ridge on the dorsolateral margin of the supraoccipital.

Present	*Sphenodon; Oplurus, Crotaphytus, Phrynosoma, Iguana, Anolis richardii;* gekkotans.
Absent	*Caiman;* agamids; chamaeleons; scincomorphs; *Varanus, Shinisaurus, Ophiodes; Trimeresurus; Diplometopon*

- Muscle related to this area

Rectus capitis (insertion).

- Traces of muscle on the bone

The rectus capitus inserts on the lateral edge of the supraoccipital, and sometimes results in the appearance of a shallow ridge (Fig., 10.1.2). The absence of the ridge does not reflect the absence of the muscle, but the presence of the ridge may be related to muscle thickness. The rectus capitus has different ways of

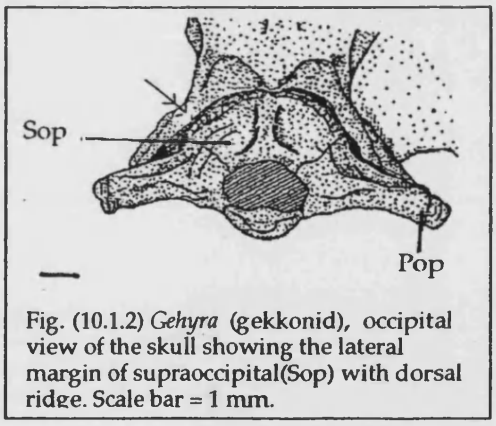
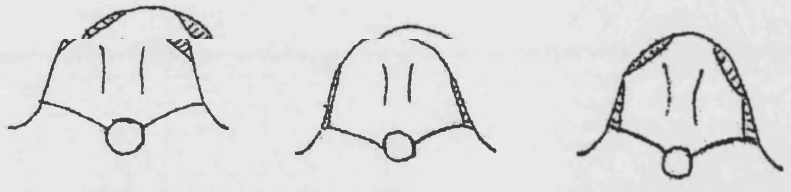


Fig. (10.1.2) *Gehyra* (gekkonid), occipital view of the skull showing the lateral margin of supraoccipital(Sop) with dorsal ridge. Scale bar = 1 mm.

inserting on the lateral side of the supraoccipital, but these do not seem to affect the presence or absence of the ridge. The table below shows the various positions of insertion of rectus capitus:

Dorsal	*Oplurus, Iguana, Crotaphytus;* gekkonids; *Varanus, Ophiodes; Ameiva.*
Ventral	*Caiman; Anolis richardii, Phrynosoma, Uromastyx* –juvenile; *Trimeresurus; Diplometopon.*
Dorsal and ventral	*Sphenodon; Calotes, Uromastyx*-adult; chamaeleons; *Uroplatus, Eublepharis; Shinisaurus;* scincids, cordylids, lacertids, *Kentropyx calcarata.*



(a) (b) (c)

Fig. (10.1.3) Sketch drawings of the occipital view in reptiles showing the effect of rectus capitis insertion a) dorsal insertion; b) ventral insertion; c) dorsal & ventral insertion.

5) The presence or absence of a dorsal ridge of the paroccipital process

Present	Gekkotans; *Oplurus, Iguana, Crotaphytus, Phrynosoma*
Absent	*Caiman; Sphenodon; Anolis richardii, Uromastyx;* chamaeleons; Scincomorpha; *Varanus, Shinisaurus, Diploglossus; Trimeresurus; Diplometopon*

Note: most agamids, *Elgaria* or *Heloderma* were not examined for this feature.

- Muscle related to this area

  Obliquus capitus (insertion).

- Traces of muscle on the bone

  The obliquus capitus inserts on: the paroccipital process (most groups); close to the suture with the supraoccipital (*Sphenodon, Shinisaurus*); the paroccipital

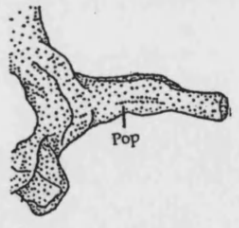


Fig. (10.1.4) *Phrynosoma asio* (iguanid), occipital view of the braincase showing the dorsal ridge on the paroccipital process (Pop). Scale bar = 1 mm.

process and quadrate (*Uroplatus*); or the paroccipital, supratemporal and parietal (*Scincus*). Where the muscle inserts as a flat layer on the dorsal edge of the paroccipital (e.g. gekkotans and some iguanians), a dorsal shelf or ridge is sometimes apparent (Fig., 10.1.4). The absence of the ridge does not always mean the absence of the obliquus capitis attachment, but may be related to the muscle thickness and the manner of attachment.

---

6) The presence or absence of the paroccipital epiphyses.

Present	Gekkotans; *Varanus*
Absent	*Caiman; Sphenodon;* agamids; chamaeleons; scincomorphs; *Heloderma, Shinisaurus, Ophiodes, Diploglossus; Trimeresurus; Diplometopon*

- Muscle related to this area

  Episternocleidomastoid muscle.

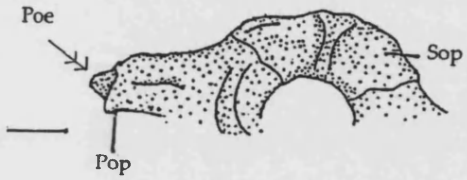


Fig. (10.1.5) *Gehyra* (gekkonid), occipital view of the skull showing the presence of the paroccipital epiphysis (Poe). Scale bar = 1 mm.

- Traces of muscle on the bone

  The episternocleidomastoid inserts on various parts of the skull (Lepidosauria) or on the cervical vertebra (*Caiman*). If the paroccipital epiphyses are present then the muscle inserts on them laterally (e.g. gekkonids - Fig., 10.1.5) . In *Eublepharis*, the episternocleidomastoid and depressor mandibulae internus both attach to the paroccipital epiphyses.

---

7) The shape of the ventrolateral margin of the oto-occipital

Convex	*Anolis richardii, Iguana; Agama; Chamaeleo chamaeleon, Chamaeleo jacksonii, Chamaeleo dilepis; Varanus; Trimeresurus; Tarentola, Phelsuma, Chondrodactylus, Gekko gecko, Diplodactylus caudicinctus, Uroplatus fimbriatus.*
Straight	*Anolis biporcatus, Crotaphytus, Oplurus; Uromastyx microlepis* (juvenile), *Ceratophora, Moloch, Draco, Phrynocephalus, Pogona; Chamaeleo vulgaris; Hemidactylus, Gehyra, Gekko smithii, Ptychozoon, Eublepharis; Lacerta trilineata; Shinisaurus; Ophiodes.*
Concave	*Sphenodon; Phrynosoma; Calotes, Uromastyx microlepis* - adult; scincids, cordylids, *Lacerta lepida,* teiids; *Heloderma; Elgaria, Diploglossus; Diplometopon.*

Note: in *Caiman*, the area was hard to interpret.

- Muscle related to this area

  Intercentral (hypapophyses) to oto-occipital muscle slips (insertion).

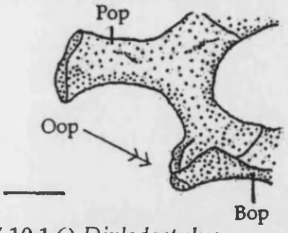


Fig. (10.1.6) *Diplodactylus* (gekkonid), occipital view of the braincase showing the convex ventrolateral margin of oto-occipital (Oop). Scale bar = 1 mm.

- Traces of the muscle on the bone

  The lateral margins of the oto-occipital are sometimes expanded (convex), possibly in relation to the insertion of the intercentral to oto-occipital muscle slips (iguanians, *Varanus* and *Trimeresurus*), although this is not the case in all taxa with a convex lateral shape (e.g. gekkonids – Fig. 10.1.6). However, where the intercentral muscle slips insert on the ventral side of the oto-occipital or under the basal tubera (most Squamata), the edge of the oto-occipital is always straight or concave.

---

8) The presence or absence of a crista tuberalis along the ventrolateral margin of the oto-occipital.

Present	Iguanids; agamids; chamaeleons; gekkotans; *Shinisaurus*; *Varanus*; *Trimeresurus*, *Diplometopon*
Absent	*Caiman*; *Sphenodon*; scincomorphs; anguids; *Heloderma*

- Muscles related to this area

  Longissimus capitis minor (insertion).

  Posterior intercentral to oto-occipital muscle slips (insertion)

  Longissimus capitis 4.

- Traces of muscle on the bone

  The crista tuberalis is a prominent crest present in many, but not all, squamates. It has an important role in supporting the compensatory

window (secondary tympanic membrane) of the ear (Baird, 1970), but may also give attachment to muscles (e.g. posterior intercentral muscles, and the longissimus capitis 4 and minor in gekkotans and *Shinisaurus*).

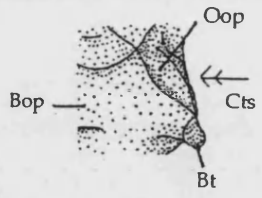


Fig. (10.1.7) *Chondrodactylus* (gekkonid), ventral view of the skull showing oto-occipital with crista tuberalis (Cts). Scale bar = 1 mm.

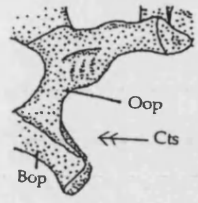


Fig. (10.1.8) *Calotes* (agamid), occipital view of the braincase showing the oto-occipital with crista tuberalis(Cts). Scale bar = 1 mm.

However, the relationship between the muscles and crest is clearly a complex one. The crest may be present (e.g. varanids, agamids, iguanids and gekkonids - Fig., 10.1.7-8), but the longissimus capitis minor inserts elsewhere, or the crest may be absent (many scincomorphs), despite the attachment of the muscle in equivalent position. This suggests that the shape of the crest is more intimately linked with ear function than muscle attachment.

9) The shape of the ventrolateral tip of the oto-occipital near its junction with the basal tubera.

Convex	*Phrynosoma*; gekkonids; lacertids; teiids; anguids
Concave	*Sphenodon*; *Oplurus*, *Anolis richardii*, *Iguana*, *Crotaphytus*; agamids; chamaeleons; *Uroplatus*, *Eublepharis*; scincids; cordylids; *Shinisaurus*; *Varanus*; *Diplometopon*; *Trimeresurus*.

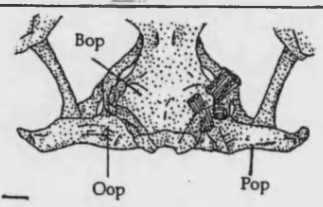


Fig. (10.1.9) *Gehyra* (gekkonid)ventral view of the basioccipital showing the ventrolateral tip of the oto-occipital (Oop). Scale bar = 1 mm.

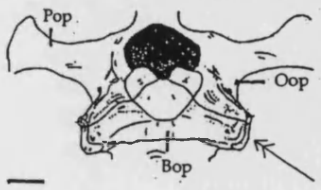


Fig (10.1.10) *Phrynosoma platyrhinos* (iguanid), occipital view of the braincase showing the ventrolateral tip of the oto-occipital (Oop). Scale bar = 1 mm.

- Muscle related to this area

  Longissimus capitis 4 (insertion)

- Traces of muscle on the bone

  Longissimus capitis 4 inserts on the ventrolateral tip of the oto-occipital in all taxa examined (Fig., 10.1.9-10), except *Sphenodon*, *Shinisaurus* and perhaps, *Caiman* where the muscle inserts on the dorsal part of the basal tubera. Therefore, enlargement of the tip clearly does not reflect the presence or absence of the muscle attachment, although a strongly convex shape might be related to muscle strength. More work on the development and distribution of this feature is needed.

  Note: in *Caiman*, the area was hard to interpret.

---

10) The presence or absence of a curved ridge on the ventral side of the oto-occipital near the occipital condyle

Present	anguids; chamaeleons; *Uroplatus*; scincomorphs
Absent smooth	*Caiman*; *Sphenodon*; iguanids; agamids; gekkonids, *Eublepharis*; *Varanus*, *Heloderma*, *Shinisaurus*; *Trimeresurus*; *Diplometopon*.

- Muscle related to this area

  Posterior intercentral to oto-occipital muscle slips (insertion)

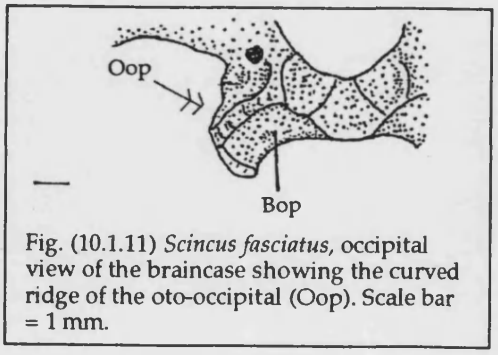


Fig. (10.1.11) *Scincus fasciatus*, occipital view of the braincase showing the curved ridge of the oto-occipital (Oop). Scale bar = 1 mm.

- Traces of muscle on the bone

  The muscles insert on the ventral side of the oto-occipital near its ventromedial border with the basioccipital. They may leave a weak curved ridge or no trace (smooth). The presence of the ridge is therefore presumably related to the manner and strength or thickness of the muscle insertion (Fig., 10.1.11).

Presacral vertebral column

1) The depth of the first intercentrum

	Flat intercentrum	Shallow intercentrum	Deep intercentrum
One muscle layer	*Caiman*, *Sphenodon*	*Heloderma*	Gekkotans, *Varanus*, *Shinisaurus*, anguids, *Trimeresurus*, *Diplometopon*
Two muscle layers superficial & deep			Iguanids, agamids, chamaeleons, scincomorphs.

- Muscle related to this area

  First intercentral to basioccipital and oto-occipital muscle (origin).

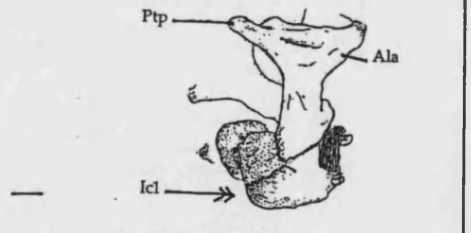


Fig. (10.1.12) *Sphenodon*, right lateral view of the atlas showing the first flat intercentrum (Ic1). Scale bar = 1 mm.

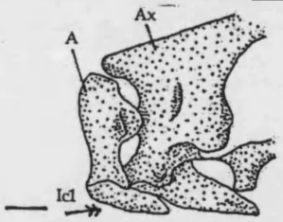


Fig. (10.1.13) *Calotes* (agamid), left lateral view of the atlas & axis showing the first deep keeled intercentrum(Ic1). Scale bar = 1 mm.

- Traces of muscle on the bone

The first intercentrum to skull muscle originates from the first (flat, shallow or keeled) intercentrum. A flat or shallow first intercentrum corresponds to a flat, thin intercentral muscle (e.g. *Caiman*, *Sphenodon* [Fig., 10.1.12], *Heloderma*). If the intercentral muscle is thick or divided (superficial and deep branches to basioccipital and oto-occipital - e.g. iguanids, agamids [Fig., 10.1.13], chamaeleons, scincomorphs), then the first intercentrum is keeled. So the thicker the muscle, the deeper the keel on the intercentrum.

---

2)The presence or absence of the proatlas

Present	*Caiman; Sphenodon*
Absent	Squamata

- Muscle related to this area

  Longissimus cervicus (insertion).

- Traces of muscle on the bone

  In *Sphenodon*, the muscle branches into anterious, which inserts on the proatlas, and posterious, which inserts on the atlas posterior process (Fig., 10.1.14).

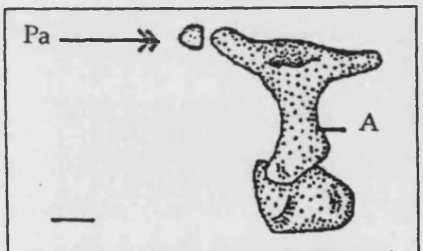


Fig. (10.1.14) *Sphenodon*, left lateral view of the atlas showing proatlas (Pa) & atlas (A). Scale base = 1 mm.

The proatlas is connected to the oto-occipital (*Sphenodon*) by tendinous tissue. In *Caiman*, the proatlas is registered as present (Goodrich, 1930; Romer, 1956; Hoffstetter and Gasc, 1969; Young, 1981), but the branches of the longus cervicus were not investigated during the dissection. By contrast, in squamates the proatlas is absent and the longus cervicus inserts on the atlas posterior process only. *Sphenodon* bears a reduced proatlas compared to other amniotes (Hoffstetter and Gasc, 1969).

Reduction of the proatlas and simplification of the longissimus cervicus muscle is therefore an advanced condition in squamates.

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3) The presence or absence of the atlas first rib

Present	*Caiman*
Absent	Lepidosauria

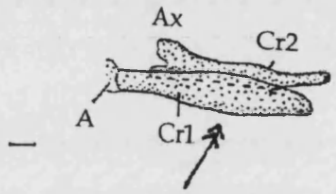

Fig. (10.1.15) *Caiman niloticus*, anterior view of the first cervical rib (Cr1) which articulates on the atlas (A). Scale bar = 1 mm.

- Muscles related to this area:

  Episternocleidomastoid (insertion).

  Iliocostalis cervicus.

  Levator scapula dorsalis and ventralis (insertion).

- Traces of muscle on the bone:

  In *Caiman*, the three muscles insert on the pointed distal end of the atlas (first) cervical rib (Fig., 10.1.15). In lepidosaurs, there is no rib on the atlas and the muscles insert either on the skull (episternocleidomastoid), or on the transverse process of the atlas (levator scapula dorsalis and ventralis, and iliocostalis cervicus) (Hoffstetter and Gasc, 1969). In man and other mammals the muscle inserts on the skull (Clemente, 1985) so this may be a primitive feature.

---

4) The shape of the posterodorsal end of the axis spine.

Triangular	*Caiman; Sphenodon;* iguanids; *Uromastyx microlepis, Ceratophora, Moloch, Draco, Calotes, Phrynocephalus; Chamaeleo vulgaris;* scincomorphs; anguimorphs; *Diplometopon.*
Oval	*Agama, Pogona; Chamaeleo jacksonii, Chamaeleo chameleon;* gekkotans; *Trimeresurus;*

- Muscle related to this area

  Spinalis cervicus (insertion).

- Traces of muscle on the bone

  The muscle runs along the posterior dorsal tips of the cervical spines, and finally inserts on the lateral side of the posterodorsal tip of the axis. The thickness and texture of the muscle affects the shape of the spine which is either triangular (thicker) in *Sphenodon* and most squamates (Fig., 10.1.16), or oval (less thick) in *Trimeresurus* and gekkotans.

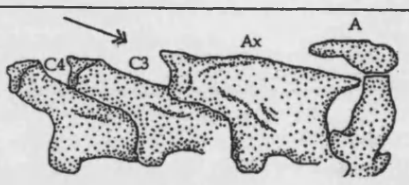

Fig. (10.1.16) *Ameiva* (teiid), right dorsolateral view of the anterior cervical vertebrae showing the triangular posterodorsal process of the C2-4. Scale bar = 1 mm.

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5) The presence of the dorsolateral crest of the axis centrum

Present	*Sphenodon*
Absent	*Caiman* and Squamata

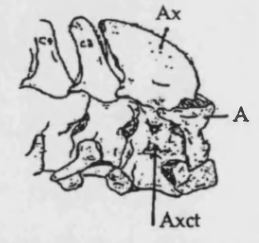

Fig. (10.1.17) *Sphenodon*, anterior lateral view of the anterior cervical vertebrae showing the axis crest (Axct). Scale bar = 1 mm.

- Muscle related to this area:

  Longissimus capitis 3 (origin).

- Traces of muscle on the bone

In *Sphenodon*, longissimus capitis 3 arises as a slip from the prezygapophyses of C3, C2 and the axis centrum (dorsolateral crest) to insert on the paroccipital process. In *Iguana* and chamaeleons, longissimus capitus 3 branches from the prezygapophyses but the axis dorsolateral crest is absent. So the origin of longissimus capitis 3 from the axis centrum, and thus presumably the crest is unique for *Sphenodon* (Fig., 10.1.17). In *Caiman* and all other taxa examined the muscle is absent.

---

6) The presence or absence of anterior tips on cervical and dorsal neural spines.

- Muscles related to this area

  Splenius capitis (insertion)

- Traces of muscle on the bone

  The muscle originates in most taxa from the anterior dorsal edge of the neural spines (cervical and sometimes dorsal). In *Sphenodon*, the muscle leaves anterior tips on the dorsal end of the spines (Fig. 10.1.25), while in other taxa, the spines are smooth. So the character is variable, but the presence of the anterior tips (*Sphenodon*) may reflect some aspect of thickness or texture of the muscle.

---

7) The presence or absence of zygosphenes and zygantra on the vertebrae

Present	*Iguana, Trimeresurus*, some lacertids
Present, rudimentary	*Sphenodon*
Absent	*Caiman*, most other Squamata (with exceptions)

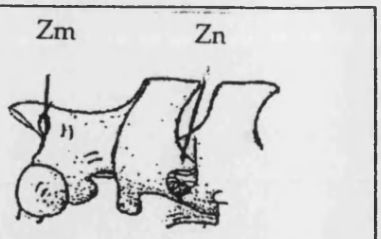

Fig. (10.1.18) *Trimeresurus albolabris*, right posterolateral view of the 11th & 12th vertebrae showing zygantrum (Zm) & zygosphenes (Zn). Scale bar = 1 mm.

The presence of a rudimentary zygosphene and zygantrum may be a primitive feature for squamates since it is present in rhynchocephalians and fossil lizards (Evans, 1994 – *Parviraptor* [rudimentary]; Wu et al., 1996 – *Sineoamphisbaenia*; Reynoso, 1998 – *Huehuecuetzpalli mixtecus* [rudimentary]. Russell (1967) and Lee (1997), also reported the presence of this articulation on mosasauroids. Estes et al. (1988), recorded the degree of development of such accessory articulations in squamates, and considered the strong development of zygosphenes and zygantra as a synapomorphy of Squamata. The figure (10.1.18) shows the well-developed zygosphenes and zygantra in the snake *Trimeresurus*.

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8) The presence or absence of a sharp edge on the posterior margin of the neural arches above the postzygapophyses

Present	*Trimeresurus*
Absent	*Caiman* and most lepidosaurs

- Muscle related to this area

  Inter-neural arch muscle slips (insertion).

- Traces of muscle on the bone

  The muscle runs as slips between the neural arches. In *Trimeresurus*, the

posteroventral edge of the arch is convex and the edges are sharp (Fig., 10.1.19). This may indicate a thicker muscle than in other Squamata (concave), but the feature needs to be examined in other snakes.

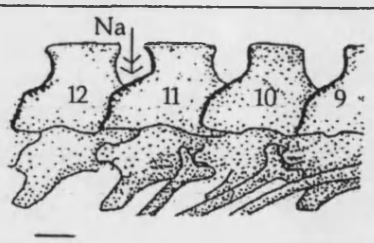

Fig. (10.1.19) *Trimeresurus wagleri*, right lateral view of the anterior vertebrae showing sharp edged neural arches (Na). Scale bar = 1 mm.

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9) The presence or absence of tubercles and posterior processes on the postzygapophyses of the cervical vertebrae

Smooth	*Caiman; Anolis edwardii, Phrynosoma;* most agamids; *Chamaeleo chamaeleon;* gekkotans; *Scincus, Tiliqua nigrolutea,* cordylids, teiids; *Heloderma, Shinisaurus, Diploglossus, Ophiodes.*
Tubercles	*Anolis richardii; Calotes; Tiliqua rugosas .*
Posterior process	*Sphenodon; Iguana; Pogona;* lacertids; *Varanus; Trimeresurus; Diplometopon.*

- Muscles related to this area

  Spinalis cervicus (insertion).

  Spinalis and semispinalis cervicus

  (insertion).

- Traces of muscle on the bone

  Both muscles attach to the cervical spines, neural arches and postzygapophyses. The postzygapophyses are usually smooth (e.g. Gekkota, many anguimorphs, and most scincomorphs), but the muscle attachment may leave posterodorsal processes (e.g. *Sphenodon, Trimeresurus, Diplometopon*), or tubercles (some iguanids and the scincid

Tiliqua rugosas). The character is thus variable within groups, but the presence of tubercles and posterior processes may be related to the thickness and/or texture of the muscle and with age or size.

---

10) The presence or absence of a wide ridge on the prezygapophyses.

Present	*Trimeresurus, Diplometopon*
absent	*Caiman, Sphenodon,* most Squamata

- Muscles related to this area

  Longissimus dorsi (insertion).

- Traces of muscle on the bone

  The muscle runs laterally along the vertebral column, attaching to the ventral side of the prezygapophyses as a series of muscle slips.

  In most lizards, the prezygapophyses have shallow ridges where the muscle slips attach. In the specimens of *Trimeresurus* and *Diplometopon* examined, the muscle leaves a wide thick ridge on the ventral side of the prezygapophyses. This presumably reflects the thickness and strength of muscle attachment in these limbless genera, but the feature needs to be examined in other taxa of snakes and amphisbaenians.

---

11) The shape of the intercentral keels

Rounded plain	*Sphenodon,* most Squamata
Rounded with lateral and central epiphyses	*Varanus*
Strongly keeled	*Ophiodes, Diploglossus; Scincus*

- Muscles related to this area

  Longus colli (origin).

Intercentral to pectoral girdle (origin).

Intercentral to posterior cervical ribs (origin).

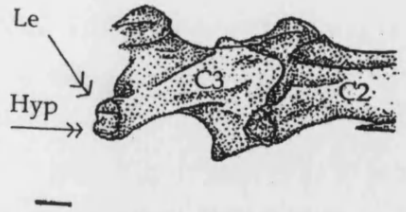

Fig. (10.1.20) *Varanus prasinus*, right ventrolateral view of the anterior vertebrae showing the special hypapophyses (Hyp) with lateral epiphyses (Le). Scale bar = 1 mm.

- Traces of muscle on the bone

  In most groups, the longus colli originates from the apices of the intercentra and extends anteriorly to insert on the basal tubera. In *Varanus* and anguids, tendinous sheets also run from the apices posteriorly to insert on the suprascapula, scapula, scapulocoracoid, clavicle (pectoral girdle), or on the cervical ribs (anguids). These additional slips affect the shape of the apices (elongated sharp keeled ends, e.g. anguids). However, in *Varanus* (also lanthanotids, Hoffstetter and Gasc, 1969), the apices have a special shape with central and lateral epiphyses (Dollo, 1884) that reflect the origin of the sheets plus the intercentral muscle slips (Fig., 10.1.20). In *Scincus*, the apices are elongated and narrow with sharp ends (like anguids), although the intercentral to pectoral girdle and cervical rib muscles are absent. In this genus, the apical enlargement is therefore due to the longus colli and cervicus muscle origin (see no. 14, and section on the ventral side of the craniocervical region).

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12) The shape of the intercentral anterolateral margins.

Deep	*Scincus, Ophiodes, Diploglossus, Varanus; Trimeresurus; Diplometopon*
Shallow	*Caiman, Sphenodon,* iguanids; agamids; chamaeleons; gekkotans; *Tiliqua;* lacertids, teiids, cordylids; *Shinisaurus, Heloderma, Elgaria, Anguis.*

- Muscles related to this area

  Longus colli (origin).

  Longus cervicus (origin).

- Traces of muscle on the bone

  The longus colli has slips from the intercentral apices and sometimes from the anterolateral margins of the intercentra (e.g. *Diploglossus* – Fig., 10.1.21). The longus cervicus originates from a deeper position on the anterolateral margins of the intercentra and inserts on the second intercentrum. Most intercentra are shallow despite the presence of longus colli and usually cervicus (except in *Caiman, Anguis fragilis,* chamaeleons). The depth of the intercentra is therefore not related to the presence or absence of longus colli and cervicus, but reflects some aspect of their thickness, extension or action.

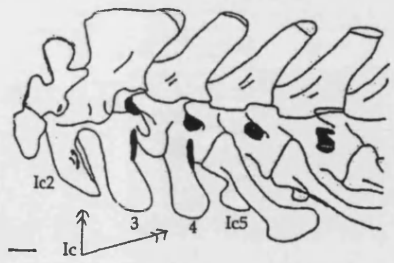

Fig. (10.1.21) *Diploglossus c. crusculus,* left lateral view of the cervical vertebrae showing deep intercentra (Ic). Scale bar = 1 mm.

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13) The presence or absence of intercentral lateral crests

Present	*Sphenodon*; gekkotans; *Scincus miternus, Gerrhosaurus,* lacertids; *Varanus; Ophiodes, Diploglossus , Shinisaurus, Elgaria*
Absent	*Caiman*; iguanids; agamids; chamaeleons;, *Scincus laterimaculatus, Tiliqua, Cordylus,* teiids; *Heloderma, Trimeresurus; Diplometopon.*

- Muscles related to this area

  Longus cervicus (insertion).

- Traces of muscle on the bone

  The longus cervicus attaches to the posterior face of the intercentra (as muscle fibres or tendons) and sometimes leaves lateral crests on the

margin. However, since the muscle may attach without leaving crests, their presence is presumably related to the angle or strength of attachment.

Intercentra that have lateral crests are:

Sphenodon, 2nd flat intercentrum and 3rd-6th keeled intercentra; Gekkota, 2nd-3rd keeled intercentra of C2 (Fig., 10.1.22); *Scincus*, 3rd intercentrum; *Gerrhosaurus*, 3rd-5th intercentra; Lacertidae, 2nd intercentrum; Varanidae, 2nd hypapophysis; *Diploglossus*, 2nd-4th intercentra; *Ophiodes*, 2nd-4th intercentra; *Shinisaurus*, 3rd-5th.

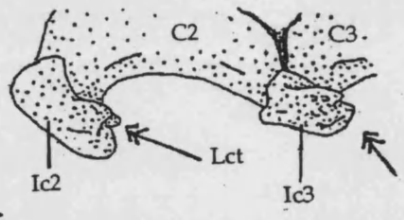

Fig. (10.1.22) *Diplodactylus* (gekkonid), left ventrolateral view of the anterior intercentra showing lateral crests (Lct) on the 2nd- 3rd intercentra. Scale bar = 1 mm.

14) The presence or absence of intercentral basal crests

Present	*Sphenodon*; gekkotans; *Scincus, Gerrhosaurus, Lacerta; Shinisaurus, Elgaria*
Absent	*Caiman*; iguanids; agamids; chamaeleons; *Tiliqua, Cordylus, Pseudocordylus, Acanthodactylus*, teiids; *Varanus, Heloderma; Diploglossus, Trimeresurus*

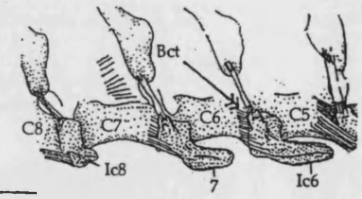

Fig. (10.1.23) *Gehyra* (gekkonid), right ventrolateral view of the posterior cervical intercentra showing basal crests (Bct). Scale bar = 1 mm.

- Muscles related to this area

  Rib ligaments (attachment).

- Traces of ligaments on the bone

  The ligaments either attach to basal crests located above the lateral crests (if present) (Fig., 10.1.23), or attach to a smooth intercentral base. The ligaments shift upwards toward the transverse process as the keeled intercentra end. So the presence of the basal crests is not directly related to the presence of the ligaments, but may be related to their thickness.

---

15) The presence or absence of a ventral mid-line keel on the cervical centra

Present	*Caiman; Sphenodon;* iguanids; *Uromastyx microlepis, Ceratophora, Moloch, Calotes, Phrynocephalus, Agama, Pogona; C. chamaeleon* (anterior centra); gekkotans; scincomorphs; *Shinisaurus* (anterior centra)
Absent smooth	*Draco; C. jacksonii, C. vulgaris, C. dilepis; Varanus, Heloderma,* anguids; *Trimeresurus; Diplometopon*

- Muscles related to this area

  Longus colli (origin and extension).

  Longus cervicus (origin and extension).

  Anterior intercentra to rib ligaments (insertion).

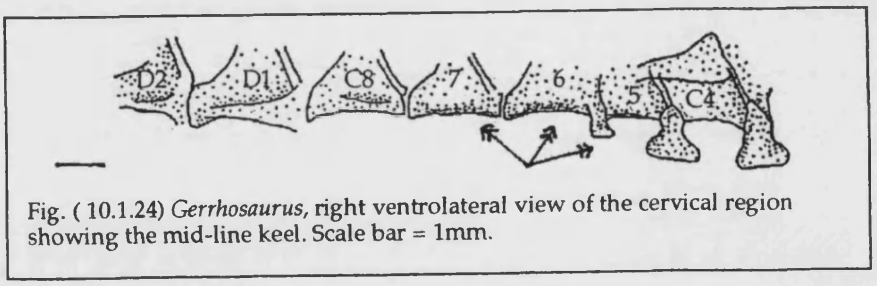

Fig. (10.1.24) *Gerrhosaurus,* right ventrolateral view of the cervical region showing the mid-line keel. Scale bar = 1mm.

- Traces of muscle on the bone

  In all examined taxa, the cervical vertebrae bear keeled intercentra between the adjacent centra. The cervical centra possess a mid-line ridge between intercentra (e.g. *Shinisaurus* and *C. chamaeleon*), and after the

disappearance of the intercentra (e.g. scincomorphs, Fig. 10.1.24). In some taxa, the ventral surface of the centra is smooth despite the presence or absence of the keeled intercentra (e.g. most chamaeleons and *Heloderma*). The longus muscles run above each other and along the cervical centra. The third muscle (anterior intercentra to rib ligaments) runs as oblique slips between the intercentra and the rib ligaments. Ventrally, the three muscles attach directly on the intercentral and central surface usually leaving a keeled mid-line ridge on the centra, although sometimes the surface of the centra is smooth. The end of the intercentra does not indicate the end of the ventral muscles, but the presence of the mid-line ridge on the centra, even after the disappearance of the intercentra, indicates the presence of ventral muscles (e.g. *Diploglossus* and *Ophiodes*). The absence or presence of the mid-ventral ridge may be related to the degree of thickness and mode of attachment of ventral muscles on the centra.

---

16) The presence or absence of parapophyseal processes

Present	*Trimeresurus*
Absent	*Caiman, Sphenodon,* most Squamata

- Muscles related to this area

  Intercentra to parapophyses and rib ligament muscle slips (insertion).

- Traces of muscle on the bone

  In *Trimeresurus*, the muscle runs deep as slips starting on the third intercentrum and inserting on the parapophyseal processes (anteriorly) and rib ligaments of vertebrae 4 and 5 (Fig., 10.1.25). The muscle continues posteriorly along the vertebral column and lies under the posterior

intercentra to rib muscle. Thus the presence of parapophyses may reflect the presence of the muscle, but this needs to be examined in other snakes.

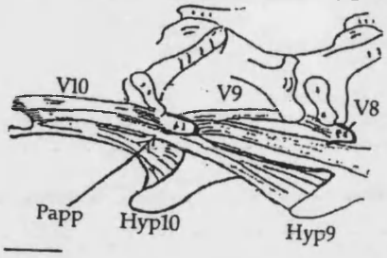

Fig. (10.1.25) *Trimeresurus albolabris*, right ventrolateral view of the anterior vertebrae showing parapophyseal processes (Papp) on the ventral side of the centra with muscle attachment. Scale bar = 1 mm.

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17) The presence or absence of anteroventral rib processes

Present	*Diplometopon*
Absent	*Caiman* and most Lepidosauria.

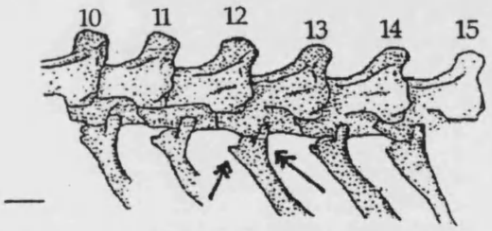

Fig. (10.1.26) *Diplometopon*, left dorsal view of the anterior vertebrae showing the anteroventral rib processes. Scale bar = 1 mm.

- Muscles related to this area

  Intercentra to rib anterior process muscles (insertion).

- Traces of muscle on the bone

  In amphisbaenian *Diplometopon*, there are short ventrolateral muscles that originate from the base of the intercentra and insert on the anterior processes of the ribs (Fig., 10.1.26). The thickness of the muscle affects the shape and size of the anteroventral process of the rib. These processes are reportedly found in all amphisbaenians, and are also present in *Dibamus* and in pygopodids (Hoffstetter and Gasc, 1969).

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18) The shape of the distal end of the ribs

Narrow	*Sphenodon*; most iguanids, *Calotes; Gerrhosaurus, Ameiva; Varanus, Heloderma, Shinisaurus, Elgaria, Anguis, Ophiodes; Trimeresurus; Diplometopon;*
Wide	*Hemidactylus flaviviridis, Tarentola, Phelsuma, Chondrodactylus, Ptychozoon, Gehyra, Uroplatus; Lacerta,* teiids, *Cordylus; Diploglossus;* most agamids; *Oplurus*
Forked	*Eublepharis, Gekko, Hemidactylus fasciatus;* scincids, *Gerrhosaurus, Acanthodactylus*

Fig. (10.1.27a) *Heloderma* , narrow distal end of cervical rib (Cr). Scale bar = 1 mm.

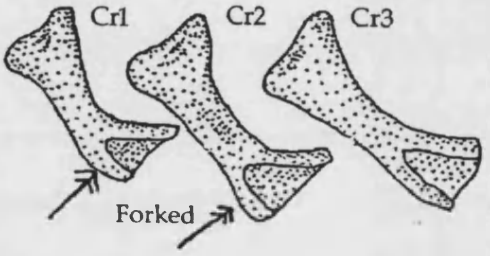


Fig. (10.1.27b) *Scincus fasciatus,* forked distal end of cervical ribs (Cr1-3). Scale bar = 1 mm.

Fig. (10.1.27c) *Gehyra* (gekkonid), right lateral view of the cervical & dorsal vertebrae showing the wide distal end of 3rd cervical rib (Cr3). Scale bar = 1 mm.

- Muscles related to this area

  Iliocostalis muscle (insertion).

  Ribs to suprascapula muscle slips (insertion).

- Traces of muscle on the bone

Evans (1981) related the compressed distal end of the cervical ribs in the primitive rhynchocephalian *Gephyrosaurus* to muscle connection between pectoral girdle and ribs. My results show that iliocostalis and ribs to suprascapula muscle slips are the only muscles attaching to the cervical ribs. Iliocostalis runs along the trunk and cervical rib shafts, while the second muscle originates from the distal ends of the cervical ribs (second, third, fourth), and inserts on the suprascapula either superficially or deep. The attachment of both muscles leaves a wide (Fig., 10.1.27c) or forked (Fig., 10.1.27b) distal end to the ribs. If forked, the posterior process is for the iliocostalis muscle slips, and the antero-ventral process is for the suprascapula muscle slips. However, the presence of the wide or forked distal ends is not directly related to the presence of the muscles, because the muscle can originate from a narrow distal end (Fig., 10.7.27a). However, the width of ribs is presumably related to the thickness and width of the muscle, or perhaps to some functional criterion. In most gekkotans (e.g. *Nephrurus*), the bifurcated ribs persist along the cervical and trunk region (Holder, 1960).

Pectoral girdle

1) Shape of the interclavicle.

Absent	Chamaeleons, *Trimeresurus, Diplometopon, Anguis fragilis*
Rod-shaped	*Caiman, Heloderma*
T-shaped	*Sphenodon, Varanus*, iguanids
Cruciform	Agamids; gekkotans; scincomorphs, *Shinisaurus*, most anguids.

- Muscles related to this area

Episternocleidomastoid (origin).

- Traces of muscle on the bone

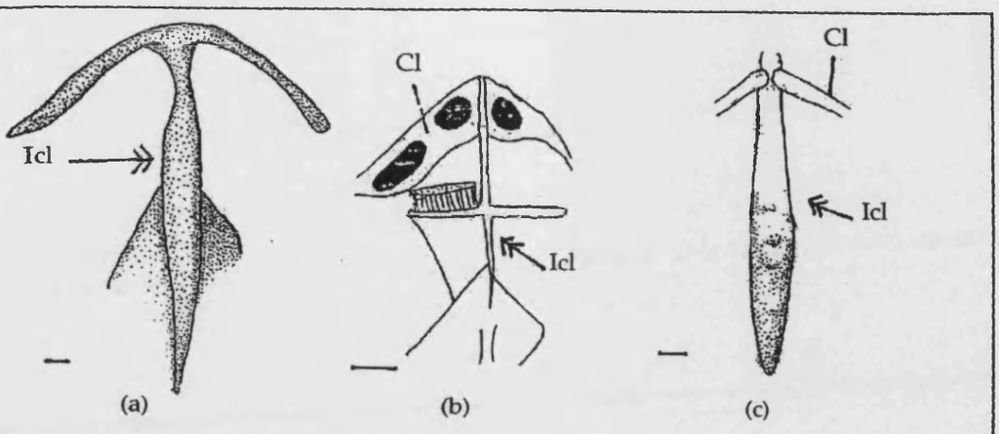


Fig. (10.1.28) Ventral view of the pectoral girdle showing the interclavicle (Icl) in a) *Varanus griseus;* T-shaped; b) *Scincus fasciatus,* cruciform; c) *Heloderma,* rod-shaped. Scale bar = 1 mm.

The interclavicle is recorded as absent in adult chamaeleons (present in embryo – Skinner, 1959), pygopodids, dibamids, amphisbaenians, snakes and some anguids (Essex, 1927; Lécuru, 1968). In all non-squamate lepidosaurs, the interclavicle has lateral processes (Fig., 10.1.28a) (T-shaped interclavicle) with rarely a small anterior process (Camp, 1923; Evans, 1981). In most scleroglossans, the anterior process is well - developed and the interclavicle becomes cruciform (Fig., 10.1.28b) (Camp, 1923; Kluge, 1967, 1987; Lécuru, 1968; Greer, 1970; Costelli and Hecht, 1971; Moody, 1980). The lateral processes of the interclavicle are absent in some taxa (Fig., 10.1.28c) (e.g. *Heloderma*, some gekkonids, gymnophthalmids - Lécuru, 1968), and this is the derived condition (Estes et al., 1988).

In most of the taxa dissected, the episternocleidomastoid muscle originates from the lateral arms of the cruciform or T-shaped interclavicle (primitive condition, Reynoso, 1998 – *Huehuecuetzpalli mixtecus*), and may have a second tendinous origin from the sternum (most scincomorphs). In some

2- The occipital surface of the skull

The skull may be divided into a number of functional components (Russell, 1967) or mechanical units (Gans, 1969b). For the purposes of this section, the relevant units are the dermatocranium (the dermal bones forming mainly the outer shell of the skull), the endocranium (braincase), the lower jaw, and the quadrate. The dermatocranium includes the parietal (skull roof), the supratemporal and the squamosal (lateral skull components), which form the outer curved shell of the occipital skull, while, the endocranium (the supraoccipital, oto-occipital, exoccipital and basioccipital) represents the braincase. The lower jaw is, of course, hinged on the skull at the quadrate – articular joint, but in many living reptiles (i.e. crocodiles and turtles), the remaining skull components are tightly connected so that the skull is rigid (akinetic, Alexander, 1968). Squamates differ in having a kinetic skull (Frazzetta, 1962), in which the braincase can move within the dermatocranium (metakinesis), the quadrate can move at its joints with the squamosal, supratemporal and pterygoid (streptostylic - Smith, 1980) and there may be an extra hinge system which permits the muzzle unit to be rotated upwards or downwards through a series of joints centred about the fronto-parietal hinge (mesokinesis). Basal lepidosaurs appear to have been metakinetic, while basal squamates were also streptostylic and, possibly, mesokinetic (mesokinesis and metakinesis lost secondarily in chamaeleons, Kardong et al., 1997).

In reptiles, there are a number of epaxial and hypaxial muscle slips that originate from, or insert on, units of the occipital region of the skull.

The craniocervical muscles mostly originate from or insert on the occipital side of the skull are:

Superficial muscles

Depressor mandibulae

Cervicomandibularis

Constrictor colli

Intermediate muscles

Episternocleidomastoid

Clavicle dorsalis

Deep muscles

Obliquus capitis

Splenius capitis and spinalis capitis

Longissimus capitis 1, 2, 3, 4 and minor

Posterior intercentral muscle slips to skull

In the following section, I will discuss the relationship between these muscles and the occipital surface of the skull. For more details tables 10.2.1 – 10.2.2 – 10.2.3 – 10.2.4 show the origin and insertion of neck muscles on and from the dermatocranium (parietal, supratemporal and squamosal), quadrate, and endocranium (braincase).

Superficial muscles

Depressor mandibulae

In most taxa examined, the depressor mandibulae (internus and externus) originates from the dermatocranium and/or quadrate (skull outer shell), except in *Diplometopon* where it arises from the endocranium (oto-occipital – see chapter 8), and *Eublepharis* where it originates from both endocranium (paroccipital epiphyses), dermatocranium (parietal, lateral skull components),

and quadrate (see chapter 5). In *Trimeresurus*, the muscle begins from the fascia of splenius capitis.

In all taxa examined, the components of depressor mandibulae extend ventrally as one united muscle bundle (overlapping), except in Agamidae* where they are separated (Fig. 10.2.1a).

Usually, the depressor mandibulae internus inserts anterior to the externus with the two slips overlapping each other on the posterior edge of the retroarticular process, but in *Caiman*, some agamids and Chamaeleonidae they insert in series (Fig. 10.2.1b).

Cervicomandibularis

In all taxa examined, the cervicomandibularis originates from the fascia of splenius capitis and inserts on the retroarticular process, except in *Diplometopon* where it inserts on the dermatocranium (parietal) and lower jaw (dentary).

Constrictor colli

In most taxa examined, the constrictor colli inserts on the fascia of splenius capitis, but in Varanidae it attaches to the endocranium (paroccipital process) and muscle fascia.

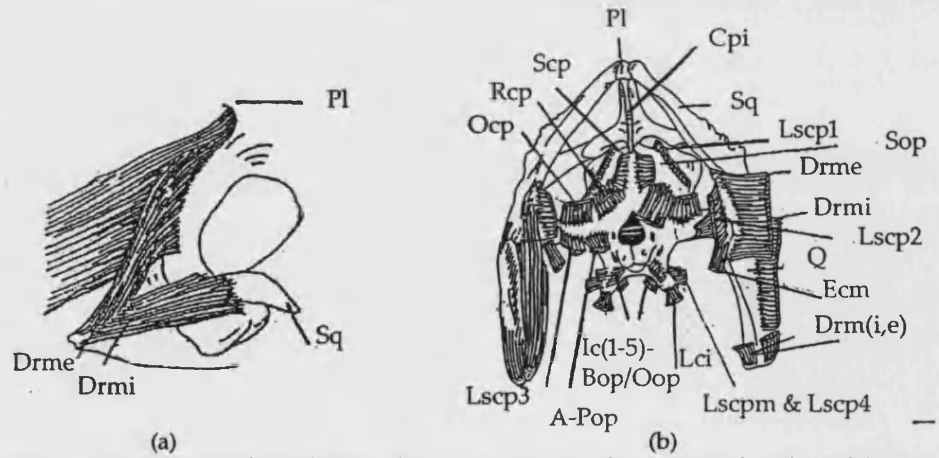


Fig. (10.2.1) a) Right posterolateral view of the skull showing the separate bundles of depressor mandibulae externus & internus (Drmi & e) in *Pogona* (agamid); b) Occipital view of the skull in *Chamaeleo chamaeleon* showing the series insertion of depressor mandibulae internus and externus (Drm[i, e]). Scale bar = 1mm.

Intermediate muscles

Episternocleidomastoid

The episternocleidomastoid originates from the pectoral girdle and extends anteriorly and obliquely to insert on the dermatocranium (parietal + lateral skull components, e.g. scincomorphs [Fig. 10.2.2a]) or endocranium (most taxa examined, e.g. gekkotans [Fig. 10.2.2b], anguimorphs), except in *Sphenodon* (parietal, squamosal and paroccipital process) and *Uromastyx* (parietal and paroccipital process) where the muscle inserts on both dermatocranium and endocranium. In *Caiman*, the episternocleidomastoid inserts on the atlas rib, while in *Trimeresurus* it is absent.

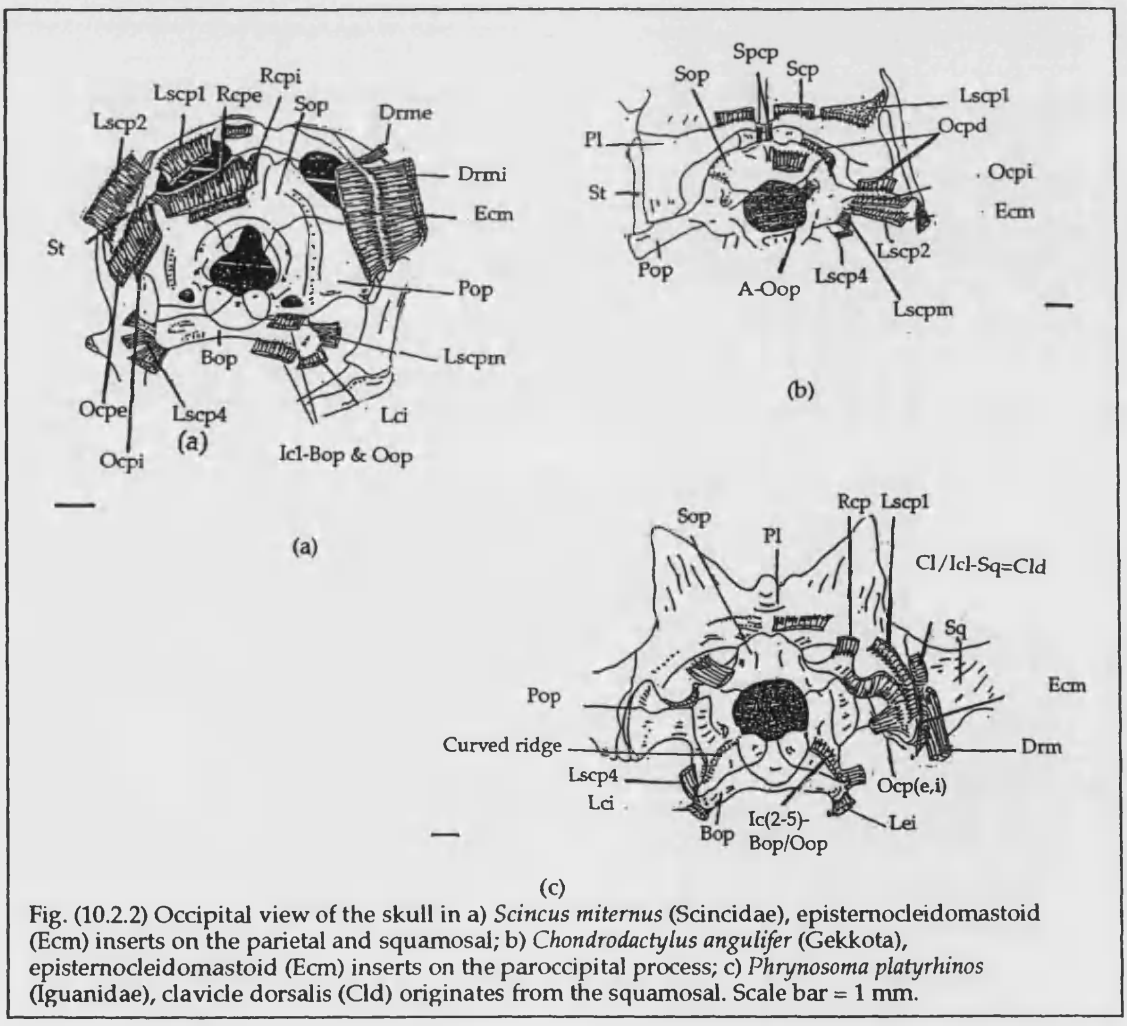


Fig. (10.2.2) Occipital view of the skull in a) *Scincus miternus* (Scincidae), episternocleidomastoid (Ecm) inserts on the parietal and squamosal; b) *Chondrodactylus angulifer* (Gekkota), episternocleidomastoid (Ecm) inserts on the paroccipital process; c) *Phrynosoma platyrhinos* (Iguanidae), clavicle dorsalis (Cld) originates from the squamosal. Scale bar = 1 mm.

Clavicle dorsalis

If it is present, the clavicle dorsalis originates from the dermatocranium and/or fascia of splenius capitis to insert on the pectoral girdle (clavicle). For example, the muscle originates from the parietal and fascia (*Sphenodon*); from the supratemporal and fascia (*Hemidactylus*) (see chapter 5); or from the squamosal (*Phrynosoma*) (Fig. 10.2.2c).

Deep muscles

Obliquus capitis

In most taxa examined, the obliquus capitis inserts on the endocranium (paroccipital process), except in Scincidae where it has an extra insertion on the dermatocranium (parietal and supratemporal) (Fig. 10.2.2a), and *Uroplatus* where there is an additional attachment to the quadrate.

Splenius and spinalis capitis

In most taxa examined, the splenius originates from anterior neural spines and inserts on the dermatocranium (parietal), except in Iguanidae* where it inserts on both dermatocranium (parietal) and endocranium (supraoccipital) (Fig. 10.2.3a)., and in Chamaeleonidae where it inserts only on the endocranium (supraoccipital) (Rieppel, 1987; Rieppel and Crumly, 1997) (Fig. 10.2.1b). Spinalis capitis is found in Gekkota, *Scincus*, Xenosauridae and Varanidae, and always inserts on the dermatocranium (parietal) (Fig. 10.2.3b).

Longissimus capitis 1, 2, 3, 4 and minor

Longissimus capitis 1

In most taxa examined, the longissimus capitis 1 inserts on the dermatocranium (parietal +/- lateral skull components), but in Chamaeleonidae it inserts on the endocranium (supraoccipital), and in *Diplometopon* the muscle branches to insert

on both dermatocranium (parietal) and endocranium (otic capsule) (Fig. 10.2.4a). In *Caiman*, the muscle is absent.

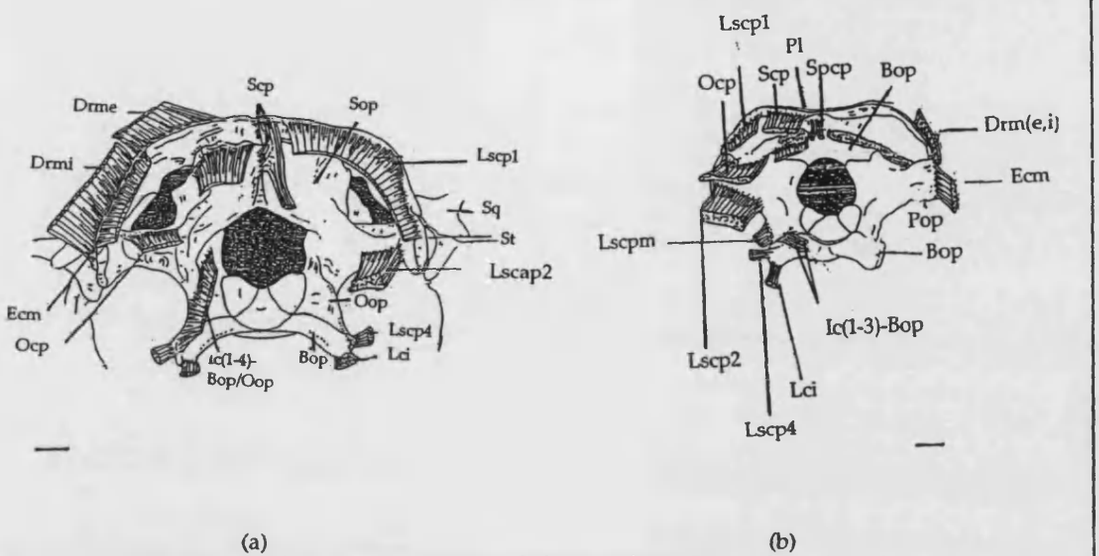


Fig. (10.2.3) Occipital side of the skull showing a) *Oplurus cyclurus* (Iguanidae), the splenius capitis (Scp) inserts on the parietal and supraoccipital; b) *Shinisaurus crocodilurus* (Anguiomorpha), the spinalis capitis (Spcp) inserts on the parietal. Scale bar = 1 mm.

Longissimus capitis 2

In most taxa examined, the longissimus capitis 2 inserts on the endocranium (paroccipital process), but in Chamaeleonidae and most scincomorphs the muscle has an extra attachment to the dermatocranium (lateral skull components) (Fig. 10.2.4b), and in *Scincus*, it is confined to this area (parietal and supratemporal) (Fig. 10.2.2a, see Lscp2).

Longissimus capitis 3

The longissimus capitis 3 is found only in *Sphenodon*, *Iguana* and Chamaeleonidae and inserts on the endocranium (paroccipital process) (Fig. 10.2.4c).

Longissimus capitis 4

In most taxa examined, longissimus capitis 4 inserts on the endocranium

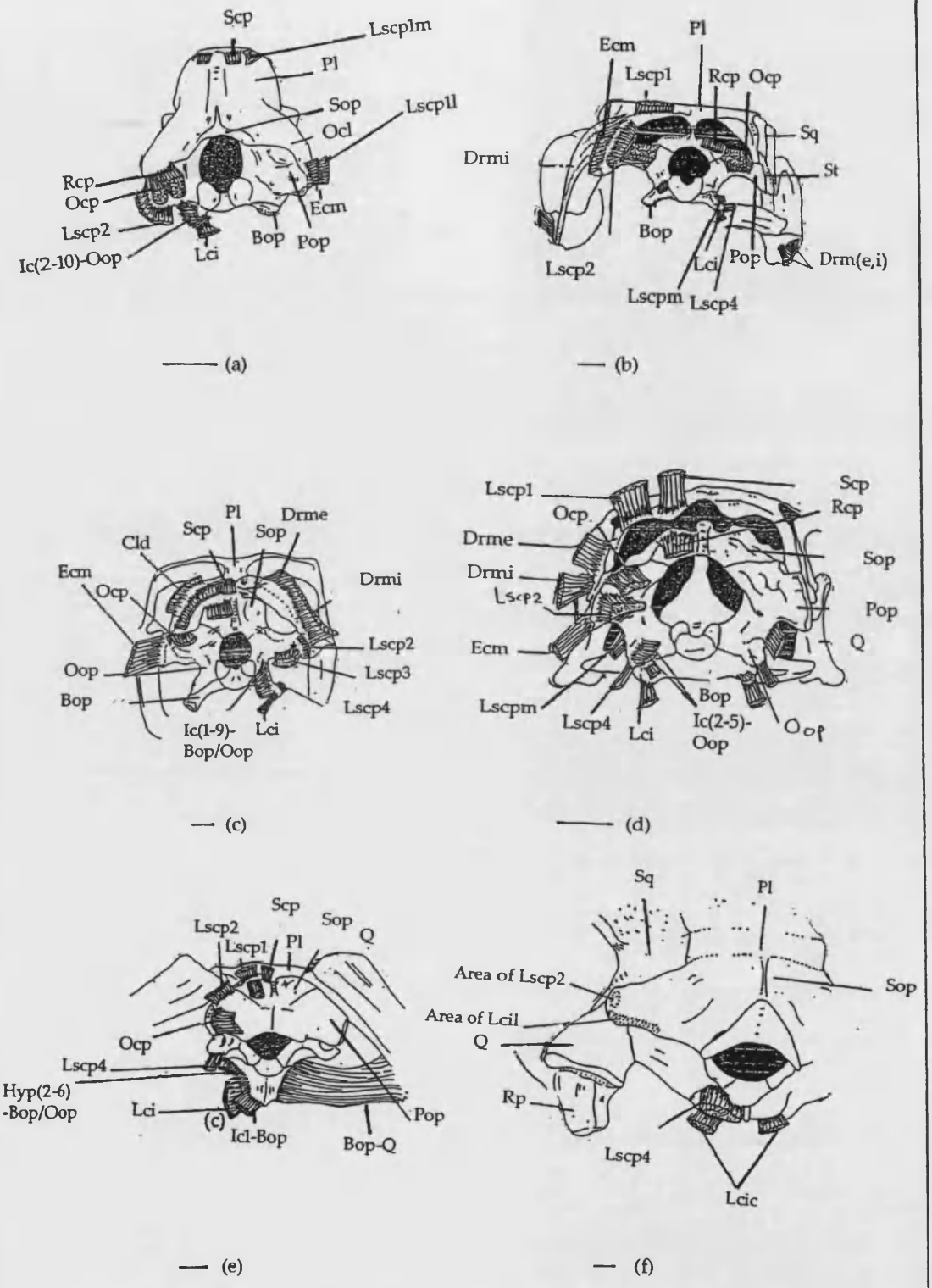


Fig. (10.2.4) Occipital view of the skull showing a) *Diplometopon zarudnyi* (Amphisbaenia), longissimus capitis 1 branches into medialis and lateralis (Lscpm & Lscpl); b) *Cordylus polyzonus* (Cordylidae), longissimus capitis 2 (Lscp2) inserts on the parietal, supratemporal and paroccipital process.; c) *Iguana iguana* (Iguanidae), longissimus capitis 3 (Lscp3) inserts on the paroccipital; d) *Ophiodes intermedius* (Anguidae), longissimus capitis 4 (Lscp4) inserts on the oto-occipital; e) *Trimeresurus wagleri* (Serpentes), longissimus capitis minor (Lscpm) is absent; f) *Caiman crocodilus*, longissimus capitis minor (Lscpm) is absent. Scale bar = 1 mm.

(basioccipital and/or oto-occipital) (Fig. 10.2.4d), except in *Diplometopon* where it inserts on the dentary.

Longissimus capitis minor

Longissimus capitis minor was found in most taxa examined and inserts on the endocranium (basioccipital and/or oto-occipital). In *Caiman*, *Sphenodon*, *Trimeresurus* and *Diplometopon* it is absent (Fig. 10.2.4e, 10.2.4f).

Intercentral muscle slips to skull

In all taxa examined, intercentral muscle slips insert on the endocranium such that the first intercentral muscle slip inserts on the basioccipital, while posterior intercentral muscle slips insert on the basioccipital and/or oto-occipital (Fig. 10.2.5a, b). In *Caiman*, posterior intercentral muscle slips are absent (Fig. 10.2.4f)

Note: Other deep muscles, such as rectus capitis and the atlas to oto-occipital insert on the endocranium.

Thus in most taxa examined, the superficial and some deep craniocervical muscles originate from or insert on the dermatocranium, while the majority of intermediate and deep muscles originate from or insert on the endocranium.

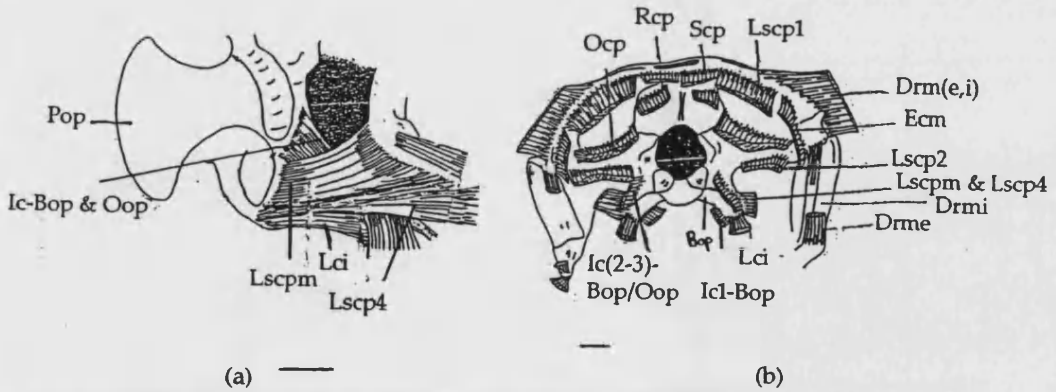


Fig. (10.2.5) occipital view of the skull showing a) *Phrynosoma platyrhinos* (Iguanidae), longissimus capitis minor (Lscpm) inserts dorsal to longissimus capitis 4 (Lscp4) and intercentral muscle slips to skull insert on the basioccipital and oto-occipital (Ic-Bop & Oop); b) *Uromastyx aegyptia* (Agamidae), intercentral muscle slips to skull insert on the basioccipital and oto-occipital (Ic2-3-Bop/Oop). Scale bar = 1 mm.

Craniocervical muscles and active metakinesis

The differences in the origin and insertion of muscles on the occipital surface of the skull (dermatocranium, quadrate or endocranium) may be related to differences in skull movements among taxa. This requires experimental confirmation, but would agree with Russell (1967) and Gans (1969b) who both assert that structural components of the skull are mechanically influenced by the attachment of ligaments and muscles. From the three graphs (Fig. 10.2.6; 10.2.7; 10.2.8), the highest proportion of muscles insert on the endocranium (braincase) in *Caiman*, *Sphenodon* and iguanians, while in Scleroglossa more muscles insert on dermatocranium (skull roof and lateral skull components). The most specialised example within iguanians is of chamaeleons, which have several unique morphological and behaviour features in comparison with other lizards. They range in habitat from humid forest areas (on trees and shrubs - arboreal) to bushes, grass, or ground-dwelling in sand dunes. The skull rises above the neck forming the casque which varies in shape (flat or pointed). The casque area is composed of bony crests and occipital lobes, and the short neck region (five cervical vertebrae) is covered externally by dorsal crests (Necas, 1999). The casque assists in nest digging (females) or display during the breeding season (male) (Singh et al., 1984). Dorsally, the casque (reduced parietal) lacks any attachment of deep axial muscles, and this probably limits movement of that area. However, some superficial adductor muscles (e.g., depressor mandibulae externus) originate from the dorsal process of the triradiate squamosal (Digastric muscle – Mivart, 1870). Detailed studies by Wahaba et al. (1992b) on the craniocervical region of *Chamaeleon vulgaris* revealed that dorsal cervical muscles such as splenius capitis and longissimus capitis 1, which normally elevate the

Summary

1) The endocranium (braincase) is mostly involved with muscle insertion, while the dermatocranium and quadrate (dorsal and lateral margins of the skull) serve as points of both origin and insertion. Thus braincase and neck vertebrae form a strong unit.

2) The numbers of muscles inserting on the dermatocranium (skull margins) and quadrate rather than the endocranium (braincase) increases dramatically in scleroglossans, and particularly scincomorphs. Active kinetic joints have been reported in many major lizard groups (Jollie, 1960), except Chamaeleonidae, amphisbaenians and *Dibamus* (consolidated skull for burrowing habits - Rieppel, 1982), but are most developed in Scleroglossa. Prokinesis is present only in snakes (where skull is highly kinetic [Frazzetta, 1962]), but here both meso- and metakinesis are absent and the parietal + braincase are closely united. Such kinetic mechanisms, plus the quadrate streptostylic movement in lizards, may assist in prey capture, improved jaw action and tooth orientation on the prey (Frazzetta, 1962, 1986; Rieppel, 1979, 1984, 1993), and act as a shock absorption system. Since metakinesis involves movement of the dermatocranium in relation to the endocranium (braincase), one set of muscles fixes the braincase to the rest of the axial skeleton but then a second set of more peripheral muscles are needed to lower or elevate the dermal skull. The far higher proportion of peripheral attachments in Scleroglossa may reflect more active metakinesis, and may also relate to some aspects of mesokinetic hinging (Frazzetta, 1962; Alexander, 1968; Carroll, 1988). Loss of metakinesis and consolidation of the skull in snakes and amphisbaenians explains the reduction in muscle attachment to the skull in these groups.

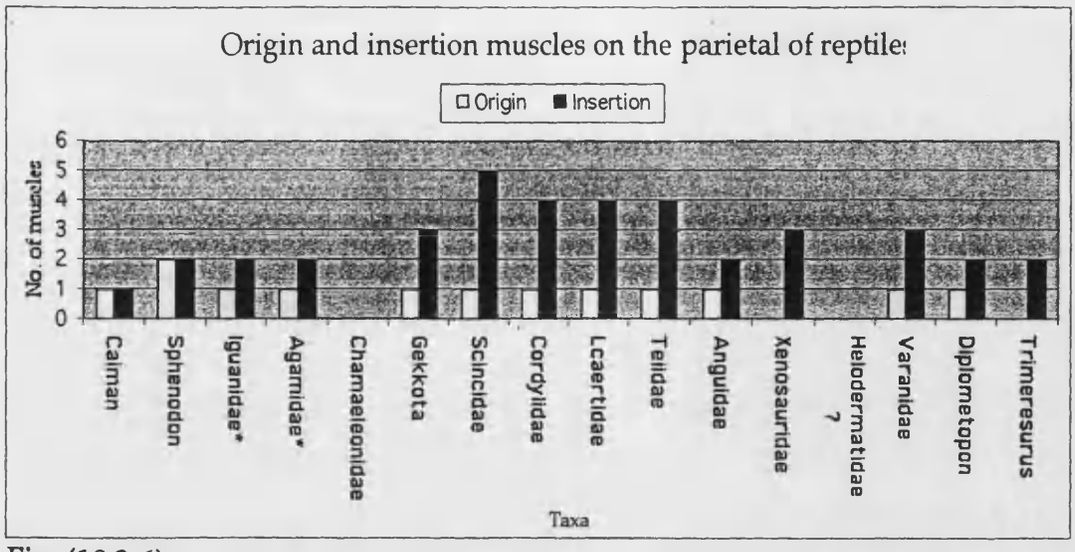


Fig. (10.2.6)

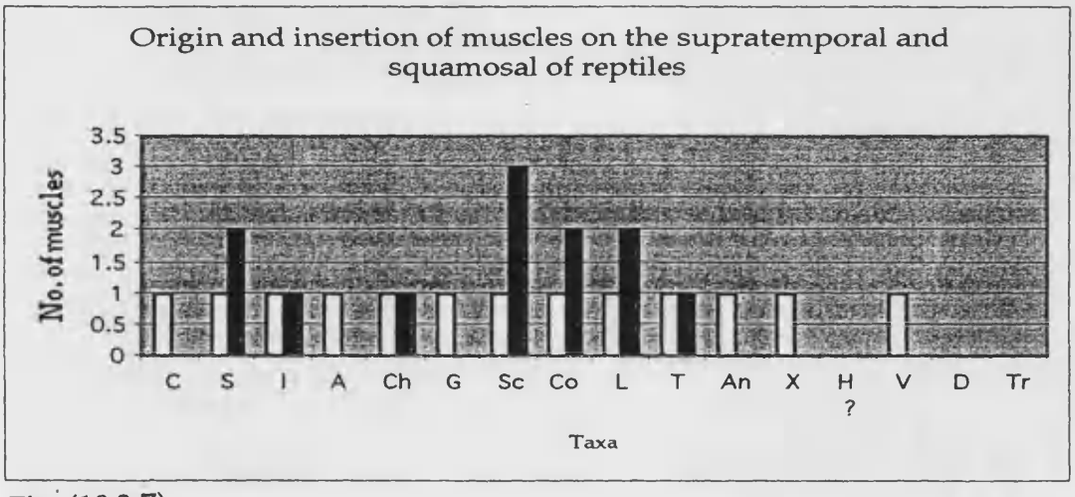


Fig. (10.2.7)

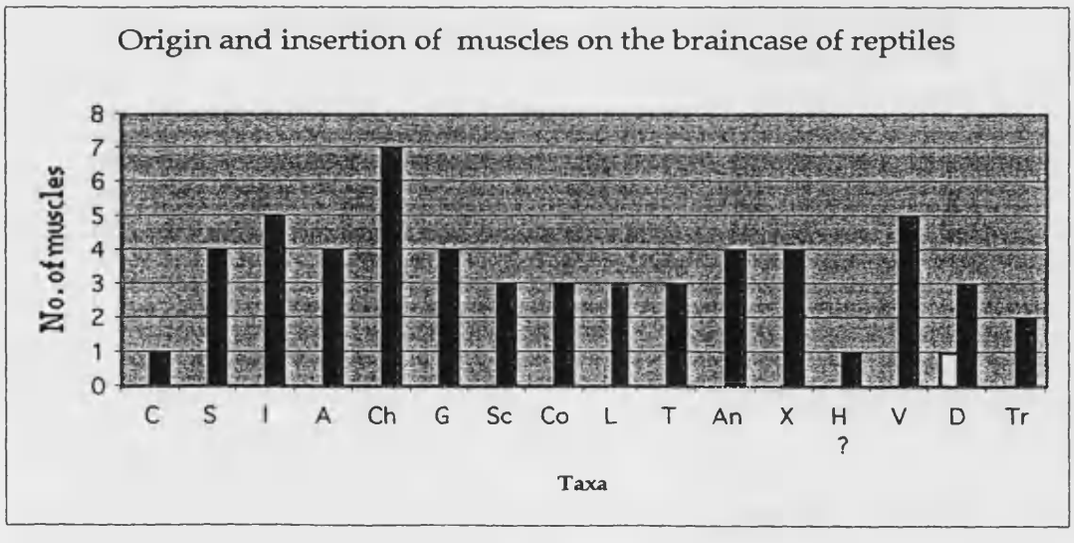


Fig. (10.2.8)

Table (10.2a) summarises the relationship between the muscles listed and the parietal.

Group	Drm	Cm	Ecm	Cld	Scp	Spcp	Ocp	Lscp1	Lscp2
Caiman	O	-	-	-	I	-	-	-	-
Sphenodon	O	-	-	O	I	-	-	I	-
Iguanidae*	O	-	-	- exp.	I	-	-	I	-
Agamidae*	O	-	- exp.	- exp.	I	-	-	I	-
Chamaeleonidae	-	-	-	-	-	-	-	-	-
Gekkota	O	-	-	-	I	I	-	I	-
Scincidae	O	-	I	-	I	- exp.	I	I	I
Cordylidae	O	-	I	-	I	-	-	I	I
Lacertidae	O	-	I	-	I	-	-	I	I
Teiidae	O	-	I	- exp.	I	-	-	I	I
Anguidae	O	-	-	-	I	-	-	I	-
Xenosauridae	-	-	-	-	I	I	-	I	-
Helodermatidae	?	?	?	?	?	?	?	?	-
Varanidae	O	-	-	-	I	I	-	I	-
Diplometopon	-	I	-	-	I	-	-	I	-
Trimeresurus	-	-	-	-	I	-	-	I	-

(O) = origin; I = insertion; (?) = not investigated; (-) = absent or not connected to the relevant region); exp. = exception, table shows usual condition within the group, but exceptions exist. Muscle abbreviations on the top row; Drm=depressor mandibulae, Cm=cervicomandibularis, Ecm=episternocleidomastoid, Cld=clavicle dorsalis, Scp=splenius capitis, Spcp=spinalis capitis, Ocp=obliquus capitis, Lscp1=longissimus capitis 1, Lscp2=longissimus capitis 2.

Table (10.2b) summarises the relationship between the muscles listed and the lateral skull components (squamosal + supratemporal).

Groups	Drm	Cld	Ecm	Ocp	Lscp1	Lscp2
Caiman (no supratemporal)	O	-	-	-	-	-
Sphenodon (no free supratemporal)	O	-	I	-	I	-
Iguanidae*	O	- exp.	I exp.	-	-	-
Agamidae*	O	-	-	-	-	-
Chamaeleonidae	O	-	-	-	-	I
Gekkota (no squamosal except eublepharids)	O	- exp.	-	-	- exp.	-
Scincidae	O	-	I	I exp.	-	I
Cordylidae	O	-	I	-	-	I
Lacertidae	O	-	I	-	-	I exp.
Teiidae	O	-	I	-	-	-
Anguidae	O	-	-	-	-	-
Xenosauridae	O	-	-	-	-	-
Helodermatidae	?	?	?	?	?	?
Varanidae	O	-	-	-	-	-
Diplometopon (no-squamosal)	-	-	-	-	-	-
Trimeresurus (no-squamosal)	-	-	-	-	-	-

(O) = origin; I = insertion; (?) = not investigated; (-) = absent or not connected to the relevant region); exp. = exception, table shows usual condition within the group, but exceptions exist. Muscle abbreviations on the top row; Drm=depressor mandibulae, Cld=clavicle dorsalis, Ecm=episternocleidomastoid, Ocp=obliliquus capitis, Lscp1=longissimus capitis 1, Lscp2=longissimus capitis 2.

Table (10.2c) summarises the relationship between the muscles and the quadrate.

Groups	Drm	Ocp
Caiman	O	-
Sphenodon	-	-
Iguanidae*	-	-
Agamidae*	O	-
Chamaeleonidae	O	-
Gekkota	- / exp.	- / exp.
Scincidae	O / exp.	-
Cordylidae	O	-
Lacertidae	O	-
Teiidae	O	-
Anguidae	O	-
Xenosauridae	O	-
Helodermatidae	?	-
Varanidae	O	-
Diplometopon	-	-
Trimeresurus	-	-

(O) = origin; I = insertion; (?) = not investigated; (-) = absent or not connected to the relevant region); exp. = exception, table shows usual condition within the group, but exceptions exist. Muscle abbreviations on the top row; Drm=depressor mandibulae, Ocp=obliquus capitis.

Table (10.2d) summarises the relationship between the muscles and the braincase.

Groups	Drm	Cstc	Ecm	Scp	Lscp1	Lscp3	Lscp4	Lscpm	(Ps)Ic
Caiman	-	-	-	-	-	-	I	-	-
Sphenodon	-	-	I	-	-	I	I	-	I
Iguanidae*	-	-	- exp.	I	-	- exp.	I	I	I
Agamidae*	-	-	I exp.	-	-	-	I	I	I
Chamaeleonidae	-	-	I	I	I	I	I	I	I
Gekkota	- exp.	-	I	-	-	-	I	I	I
Scincidae	-	-	-	-	-	-	I	I	I
Cordylidae	-	-	-	-	-	-	I	I	I
Lacertidae	-	-	-	-	-	-	I	I	I
Teiidae	-	-	-	-	-	-	I	I	I
Anguidae	-	-	I	-	-	-	I	I	I
Xenosauridae	-	-	I	-	-	-	I	I	I
Helodermatidae	?	?	?	?	?	?	?	I	?
Varanidae	-	I	I	-	-	-	I	I	I
Diplometopon	O	-	I	-	I	-	-	-	I
Trimeresurus	-	-	-	-	-	-	I	-	I

(O) = origin; I = insertion; (?) = not investigated; (-) = absent or not connected to the relevant region); exp. = exception, table shows usual condition within the group, but exceptions exist. Muscle abbreviations on the top row; Drm=depressor mandibulae, Cstc=constrictor colli, Ecm=episternocleidomastoid, Scp=splenius capitis, Lscp1=longissimus capitis 1, Lscp2=longissimus capitis 2, Lscp3=longissimus capitis 3, Lscp4=longissimus capitis 4, Lscpm=longissimus capitis minor, (Ps)Ic=posterior intercentral muscle slips.

3- The ventral side of the craniocervical region

Hoffstetter and Gasc (1969) defined the cervical region as the vertebrae anterior to the first dorsal vertebra that articulates with the sternum. In typical limbed squamates the number of cervical vertebrae ranges between 8-9, but, in some non-snake squamates the number is reduced: 4 in *Dibamus;* 4-5 in most amphisbaenians; 5 in chamaeleons; and 7 in feylinids (scincids) (Hoffstetter and Gasc, 1969). The ventral surface of the craniocervical region can be divided into two compartments: the cervical vertebrae (where most ventral muscles originate) and the basioccipital (where most ventral muscles insert).

The cervical region consists of centra, intercentra (hypapophyses), rib ligaments and ribs. The basioccipital, which is the ventral part of the braincase, bears the basal tubera.

In most recent reptiles, the cervical region has special ventral muscles: the ventral muscles include the longus colli and longus cervicus (the major two muscles that dominate the ventral side of the cervical and anterior dorsal region of the vertebral column), and the intercentral muscle slips to the skull which lie between the two muscles. The extrinsic longus colli lies ventral to the intrinsic longus cervicus. Both originate posteriorly as segments or slips of muscles from centra, intercentra and rib ligaments (Fig., 10.3.1a) and run anteriorly to insert on the axis (cervicus) or skull (colli). The longus colli can either be thick and wide (e.g. *Sphenodon,* Iguanidae*) or thin and narrow (e.g. Chamaeleonidae, *Trimeresurus*). It usually forms a single elongated bundle, but sometimes it is divided into two bundles (e.g. Iguanidae*, Agamidae*). In *Sphenodon, Scincus* and *Shinisaurus* the longus colli divides anteriorly into three bundles (medial, intermediate and lateral) (Fig., 10.3.1b). This division of longus colli may be a

primitive characteristic of lepidosaurs (*Sphenodon* and most iguanians), since in most scleroglossans examined (except *Scincus* and *Shinisaurus*) the muscle has only a single bundle.

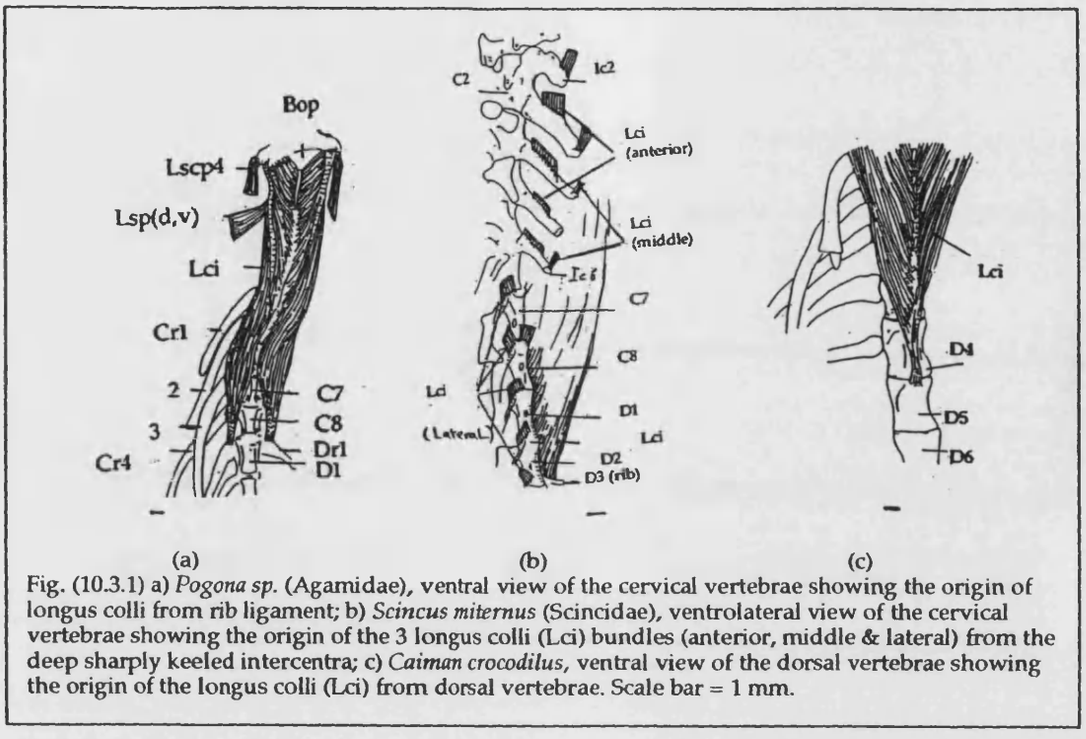


Fig. (10.3.1) a) *Pogona sp.* (Agamidae), ventral view of the cervical vertebrae showing the origin of longus colli from rib ligament; b) *Scincus miternus* (Scincidae), ventrolateral view of the cervical vertebrae showing the origin of the 3 longus colli (Lci) bundles (anterior, middle & lateral) from the deep sharply keeled intercentra; c) *Caiman crocodilus*, ventral view of the dorsal vertebrae showing the origin of the longus colli (Lci) from dorsal vertebrae. Scale bar = 1 mm.

Longus cervicus is deep and narrow by comparison to the longus colli. When present (not *Caiman*, chamaeleons, or *Trimeresurus*; reduced in most limbed anguimorphs and *Diplometopon*), it usually runs anteriorly as a series of overlapping muscle slips, each slip starting from the anterior margin of deep intercentra, and converges anteriorly to insert on the second intercentrum. It can form a single bundle (e.g. Iguanidae*, Agamidae*, Scincomorpha and some Anguidae), two bundles (e.g. *Sphenodon* and Gekkota), or three bundles (*Diploglossus*) (Fig., 10.3.2a).

The longus muscles start from either dorsal or cervical centra (Fig., 10.3.1c). Usually longus colli originates from further caudally than longus cervicus (Fig., 10.3.2b) except in *Sphenodon* and *Varanus* where the reverse occurs. In most

Gekkota, and some Iguanidae* and Agamidae*, longus colli and cervicus begin at the same level (Table, 10.3.2) (Fig., 10.3.2c), but one or both muscles may extend further caudally to make the neck either functionally longer, or be reduced in length, making the cervical region functionally shorter. Extending the muscles may give extra mobility, while shortening them may decrease flexibility but strengthen the neck.

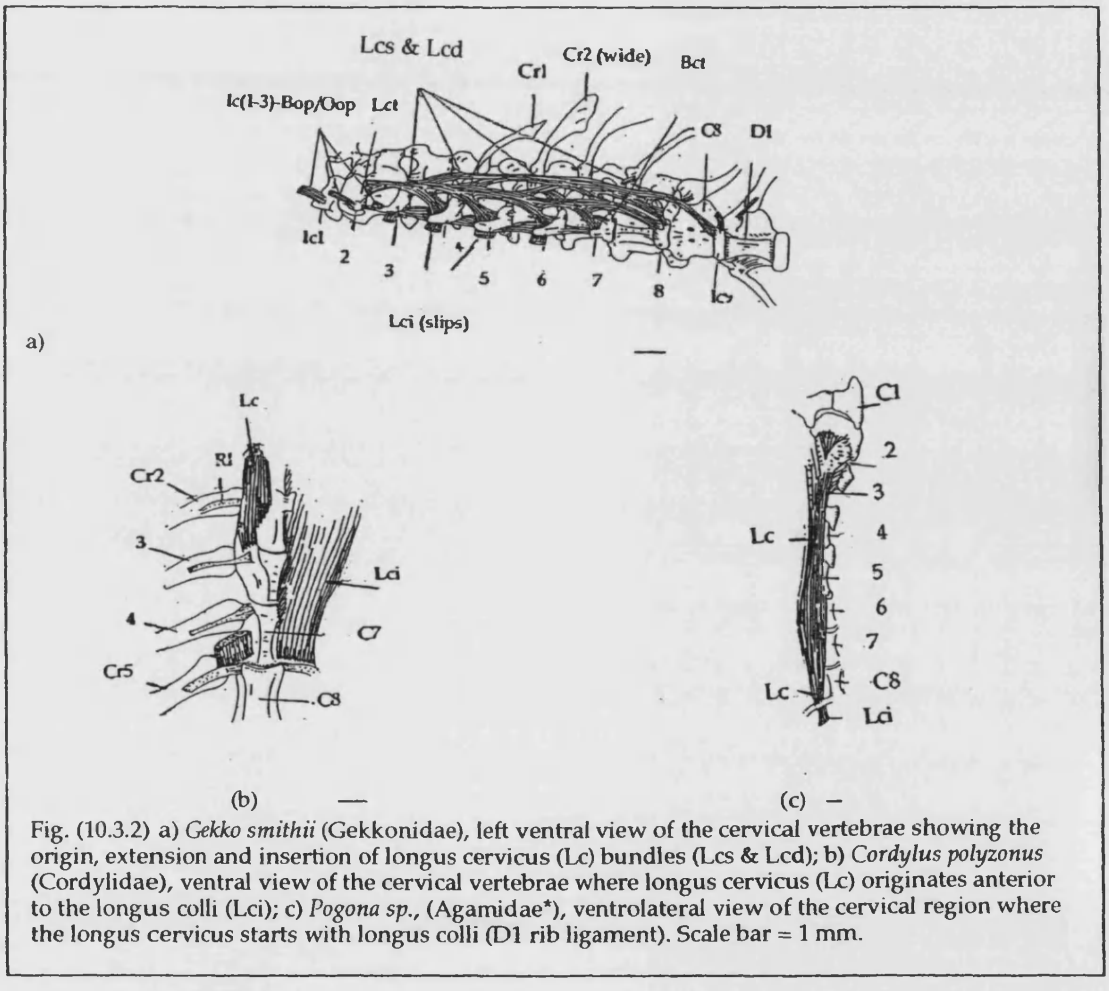


Fig. (10.3.2) a) *Gekko smithii* (Gekkonidae), left ventral view of the cervical vertebrae showing the origin, extension and insertion of longus cervicus (Lc) bundles (Lcs & Lcd); b) *Cordylus polyzonus* (Cordylidae), ventral view of the cervical vertebrae where longus cervicus (Lc) originates anterior to the longus colli (Lci); c) *Pogona sp.*, (Agamidae*), ventrolateral view of the cervical region where the longus cervicus starts with longus colli (D1 rib ligament). Scale bar = 1 mm.

The intercentral muscles to the skull are short oblique muscle slips that connect the anterior intercentra with the skull. Their presence is reflected by the development of keeled intercentra, but their number (which range from 1-10)

does not always match the number of keeled intercentra (except in *Diplometopon* [10], *Iguana* [5], *Moloch* [2] and *Chamaeleo* [2-5]).

In most limbed squamates the boundary between the cervical and dorsal region is obvious. However, the pectoral girdle is reduced in *Diplometopon* and is completely absent in *Trimeresurus*; both *Diplometopon* and *Trimeresurus* have also lost the sternal ribs. As in other limbless taxa, it is therefore impossible to separate the dorsal and cervical vertebrae. Caldwell (2000), suggested using other osteological features such as the presence, position, morphology and number of intercentra (hypapophyses). However, as Hoffstetter and Gasc (1969) reported (and this study confirms) hypapophyses are variable between and within species and cannot be used crudely to mark the limits of the neck.

The following sections explore the relationship between the features of the ventral craniocervical region including the cervical vertebrae (centra, intercentra and rib ligaments) and basioccipital, and the hypaxial muscles (like longus colli, longus cervicus and the intercentral muscle slips to the skull), which vary between taxa.

Cervical vertebrae

1) Centra:

The ventral region of the cervical centra possesses the following features:

- Mid-ventral ridge on the centrum.
- Bony processes.

- Mid-ventral ridge on the centrum:

In most taxa examined, a mid-ventral ridge occurs on the vertebral centra in the region bearing keeled cervical intercentra (Fig., 10.3.3a). When the keeled

intercentra are lost (usually in the region of posterior cervical or dorsal vertebrae), the central mid-ventral ridge usually become shallow and spreads laterally (where longus colli and cervicus muscle slips originate), and finally the central surface becomes smooth in the dorsal vertebrae (caudal to the ventral cervical muscles). This demonstrates that the mid-ventral ridge of the centra and the keeled intercentra typically occur together and may relate to some aspect of thickness and mode of attachment of ventral cervical muscles. Moreover, the retention of the central mid-ventral ridge after the last keeled intercentrum is generally correlated with the posterior extension of the ventral muscles. Some anguids show this condition, where longus colli originates on the posterior cervical (*Diploglossus*) (Fig., 10.3.3b), or anterior dorsal vertebrae (*Ophiodes*).

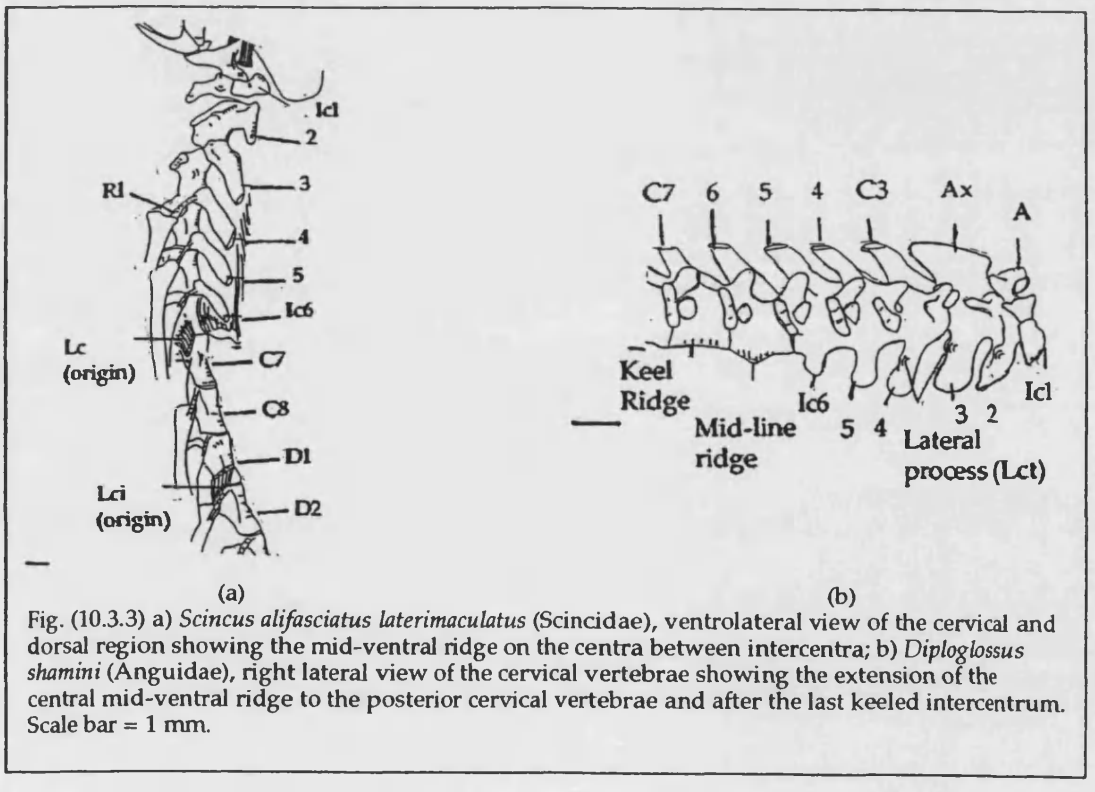


Fig. (10.3.3) a) *Scincus alifasciatus laterimaculatus* (Scincidae), ventrolateral view of the cervical and dorsal region showing the mid-ventral ridge on the centra between intercentra; b) *Diploglossus shamini* (Anguidae), right lateral view of the cervical vertebrae showing the extension of the central mid-ventral ridge to the posterior cervical vertebrae and after the last keeled intercentrum. Scale bar = 1 mm.

This indicates that ventral cervical muscles (longus colli and cervicus) begin not only from the most posterior keeled intercentrum but also from the most posterior centrum with a mid-ventral ridge. The shallow lateral ridges that appear on the centra after the last keeled intercentrum might be useful in delimiting the neck, but not in *Trimeresurus* (hypapophyses continue along much of the vertebral column) or *Diplometopon* (smooth centra after the last keeled intercentrum).

- Bony processes:

There are other bony features on the centra (e.g. processes) where deep ventral muscles attach. In *Trimeresurus*, as in most other snakes, the centra bear posterior parapophyseal processes that are located close to the transverse processes and on which deep hypapophyseal to parapophyseal muscle slips insert (Hoffstetter and Gasc, 1969; Gans, 1980) (Fig., 10.3.4). Those parapophyseal processes are also linked together by the interparapophyseal muscles. The central parapophyseal processes and their muscle slips appear anteriorly and continue posteriorly along the vertebral column towards the caudal region.

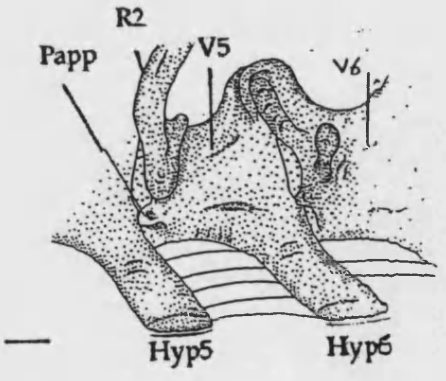


Fig. (10.3.4) *Trimeresurus albolabris*, left ventrolateral view of the anterior vertebrae showing the deep hypapophyses of vertebrae 4-5 with parapophyseal processes (Papp). Scale bar = 1 mm.

This suggests that in *Trimeresurus* the presence of the central bony processes (e.g. parapophyseal processes) is not useful in subdividing the presacral column and is functionally important in body co-ordination during locomotion (Auffenberg, 1962).

2) Intercentra:

These bony elements are usually found only between the cervical centra, except in *Sphenodon* and most gekkotans where they continue posteriorly along the rest of the presacral vertebral column (e.g. *Uroplatus*, see Fig. 10.3.4a). In *Trimeresurus* and some other snakes, the intercentra are no longer free but form fused hypapophyses that continue posteriorly along the trunk to a varying degree (Hoffstetter and Gasc, 1969; Gans, 1980).

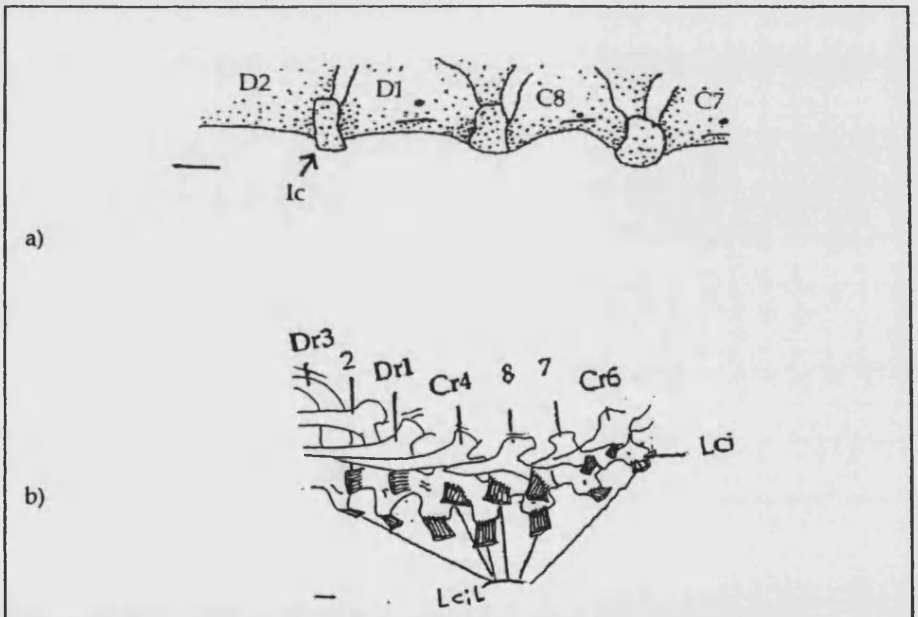


Fig. (10.3.5) a) *Uroplatus fimbriatus* (gekkonid), right ventrolateral view of the intercentra (Ic) which continue into the trunk region.; b) *Caiman crocodilus* (Crocodiles), right ventrolateral view of the cervical and dorsal vertebrae showing the longus colli lateralis (Lcil) slips originating from the ventral processes and laterally from centra. Scale bar = 1 mm.

Caiman lacks true intercentra, but has non-homologous ventral processes (Osborn, 1900; Romer, 1956; Gasc, 1961; Hoffstetter and Gasc, 1969; Gauthier et. Al., 1988) (Fig., 10.3.5b).

There is a relationship between the ventral cervical muscles (longus colli, cervicus, and intercentral muscle to skull) and the following:

- Keeled intercentra.
- Intercentral lateral and basal crests.

- Keeled intercentra:

In most taxa examined, all cervical intercentra are keeled. The exceptions are *Caiman*, *Sphenodon* and *Heloderma*, where the few cervical intercentra are flat, while *Trimeresurus* (and all snakes) have keeled intercentra (fused hypapophyses) along much of the precloacal vertebral column. In the lepidosaurs examined (except *Trimeresurus*), the number of keeled intercentra ranges from 2-10, and they vary in their size, shape and position of attachment to the centra.

In all taxa examined, ventral cervical muscles are associated mainly with ventral projections or keeled intercentra, but the position of the last keeled intercentrum does not always reflect the start of the ventral cervical muscles (except gekkotans), nor the start of the cervical region. For example, the teiids *Kentropyx calcarata* and *Ameiva ameiva* vary in the level of origin of longus cervicus (C8 or C6), although both have 6 keeled intercentra (Fig. 10.3.6, a-b).

In varanids, the longus colli begins anterior to the last keeled intercentrum, but in *Diplometopon* the same muscle begins posterior to it. There is thus usually a correlation between the origin of ventral cervical muscles and the presence of the keeled cervical intercentra, but there are exceptions and other factors may be involved.

The first intercentral muscle slip to the skull was present in all taxa examined, whether or not the first intercentrum was keeled (e.g. in *Caiman* and *Sphenodon* where the first intercentrum is flat).

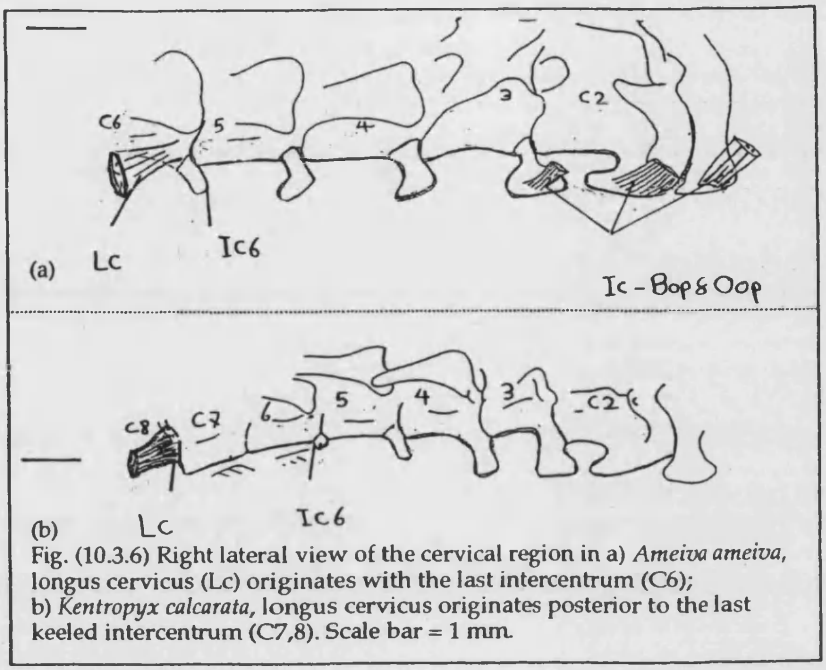


Fig. (10.3.6) Right lateral view of the cervical region in a) *Ameiva ameiva*, longus cervicus (Lc) originates with the last intercentrum (C6); b) *Kentropyx calcarata*, longus cervicus originates posterior to the last keeled intercentrum (C7,8). Scale bar = 1 mm.

Posterior intercentral muscle slips to the skull were also present in all taxa examined (except *Caiman*). In *Sphenodon* and *Heloderma*, the second intercentral muscle slip to the skull is absent and the second intercentrum is flat (Fig. 10.3.7a), while in *Chamaeleo jacksonii* and *Moloch horridum* the third intercentral muscle slip is absent, and the third intercentrum is flat. There is thus a relationship between the presence of the posterior intercentral muscle slips to the skull and keeling of the posterior intercentra, but the relationship is not exact.

In gekkotans, for example, the number of keeled intercentra range between 4-8, but the posterior intercentral muscle slips range between 1-4 (table, 10.3.1).

In most taxa examined, longus colli muscle slips originate from intercentral apices, while the cervical intercentral depth reflects the origin of longus cervicus

muscle slips. The keeled intercentra may bear accessory processes that reflect the attachment of other muscles. For example, in *Sphenodon* and *Heloderma* the second intercentrum is flat and possesses lateral crests (where longus cervicus attaches). In gekkotans the posterior intercentra (4-7) are fairly uniform (deep, narrow and pointed anteriorly) and the last reflects the start of longus colli, while their depth reflects the presence of the longus cervicus. After this the trunk region begins, the ventral muscles are absent, and the intercentra are flat. In *Trimeresurus*, the longus cervicus is absent and the depth of the hypapophyses partly reflects the oblique hypapophyses muscle slips to the rib shafts, which run along the vertebral column. The start of the ventral cervical muscles in *Trimeresurus* (longus colli and hypapophyses to rib shafts begin from the 10th hypapophysis; hypapophyses muscle slips to skull [1-6]) may mark the beginning of the trunk region.

The keeled cervical intercentra are not only shaped by the ventral cervical muscles, but also by the intercentra (or hypapophyses) to pectoral girdle muscle slips.

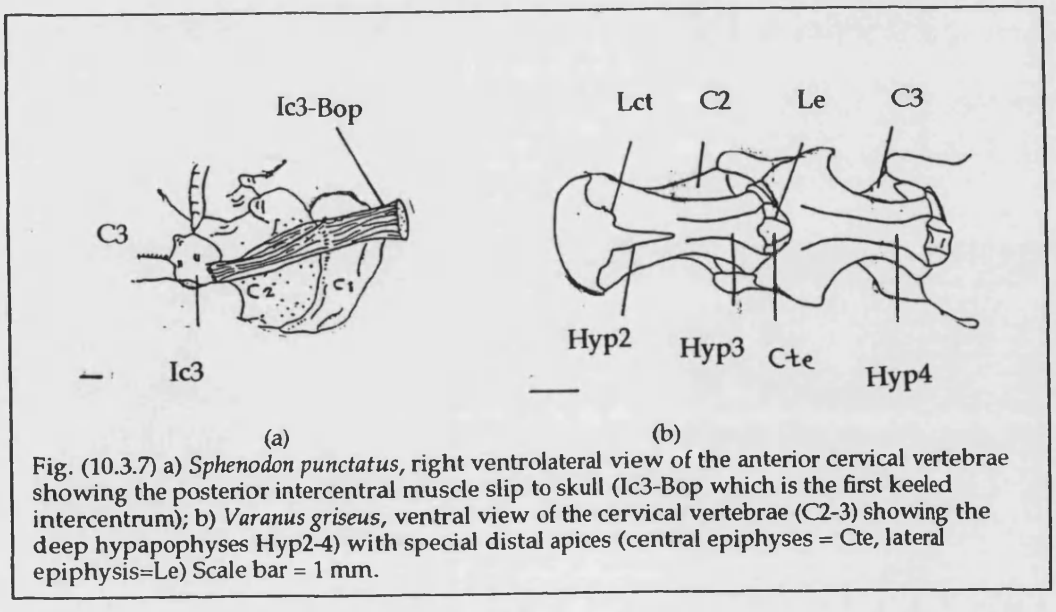


Fig. (10.3.7) a) *Sphenodon punctatus*, right ventrolateral view of the anterior cervical vertebrae showing the posterior intercentral muscle slip to skull (Ic3-Bop which is the first keeled intercentrum); b) *Varanus griseus*, ventral view of the cervical vertebrae (C2-3) showing the deep hypapophyses Hyp2-4) with special distal apices (central epiphyses = Cte, lateral epiphysis=Le) Scale bar = 1 mm.

In *Varanus*, the deep hypapophyses have specialised apices (lateral and middle epiphyses) which reflect the presence of longus colli, the reduced modified longus cervicus (long narrow tendons), and the hypapophyses to pectoral girdle and cervical rib muscle slips (Fig., 10.3.7b). In *Diploglossus shamini*, the sharp apices of the deep intercentra reflect the same double attachment.

- Lateral and basal crests on intercentra:

Most cervical intercentra possess tiny posterior crests (lateral and basal crests), which are associated with the attachment points of different muscles. The lateral crests are present on the anterior keeled intercentra and are associated with longus cervicus slips, while basal crests are present in most posterior intercentra and are associated with rib ligaments. In all lepidosaurs examined, the first intercentrum lacks both lateral and basal crests (where longus cervicus and rib ligaments are absent).

The second keeled intercentrum possesses single lateral crests in most taxa examined (e.g. *Sphenodon* [Fig. 10.3.8a], some Scincomorpha and Anguimorpha), but, most Gekkonidae have specialised intercentra with double lateral crests where the layered longus cervicus (superficial and deep) inserts. This division of longus cervicus into 2 bundles seems to be a distinctive character of gekkotans (Fig. 10.3.8b-c).

The lateral and basal crests continue along the posterior intercentra in some taxa, like *Sphenodon* (3-6 intercentra), *Gerrhosaurus* (3-5 intercentra – Fig. 10.3.8d), and gekkotans (3-8 intercentra), while only lateral crests occur in *Shinisaurus* (3-5 intercentra) and anguids (~2-4 intercentra).

Where longus cervicus is reduced to short wide tendons, the intercentra possess large lateral crests where each longus cervicus tendon connects the intercentrum with the cervical rib (e.g. *Shinisaurus* and *Elgaria*), but when longus cervicus is reduced to a long narrow tendon as in *Diplometopon* (2-7 intercentra), the lateral crests are absent and the central surface is smooth.

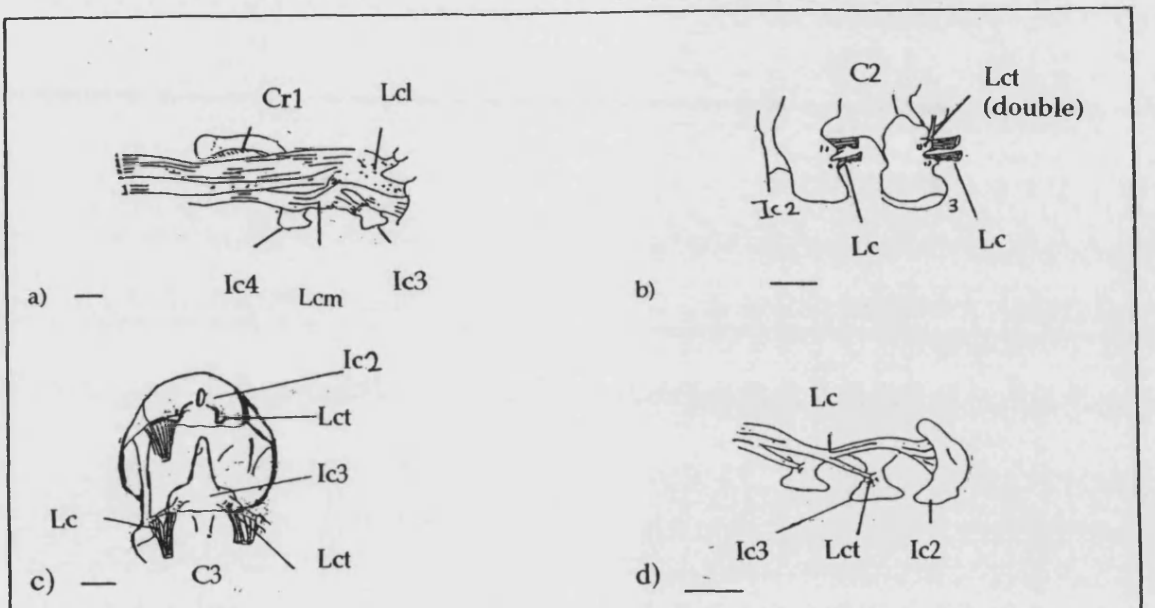


Fig. (10.3.8) a) *Sphenodon punctatus*, right ventrolateral view of the anterior cervical vertebrae showing the extension of longus cervicus (Lc) as 2 bundles lateralis and medialis (Lcl & Lcm) inserted on the 2nd intercentrum; b) *Gekko gecko*, left ventrolateral view of the cervical vertebrae showing 2nd & 3rd intercentra with double lateral crests (Lct); c) *Tarentola mauritanica*, ventral view of the anterior cervical vertebrae showing single bundle of longus cervicus (Lc); d) *Gerrhosaurus flavigularis*, right ventrolateral view of the anterior cervical vertebrae showing lateral crests (Lct) which continue posteriorly. Scale bar = 1 mm.

Thus the presence, number, and degree of development of intercentral lateral and basal crests reflect the presence, division and thickness of longus cervicus and rib ligaments. In all taxa examined, longus cervicus starts from cervical +/- dorsal vertebrae and inserts on the anterior intercentra (lateral crests), while the cervical rib ligaments attach to the basal crests of cervical intercentra. Therefore, the presence of basal crests on the intercentra may assist in the delimitation of the neck region (Fig., 10.3.2a, 10.3.5a).

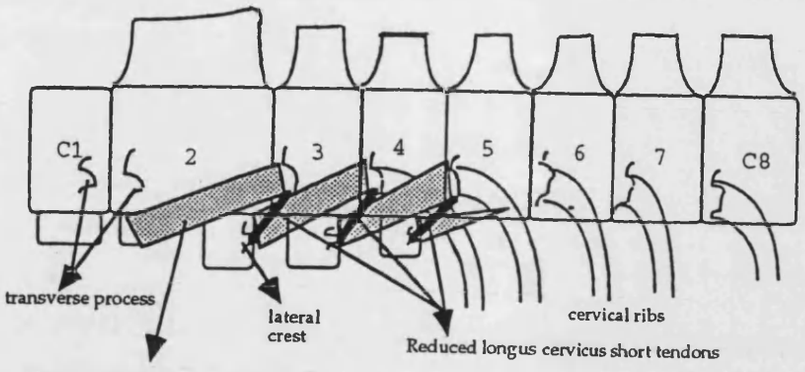


Diagram (10.3.1) left lateral view of the cervical vertebrae showing the large lateral crests where thick short tendons attach to both crests and transverse processes. The tendons probably represent the reduced longus cervicus in *Shinisaurus crocodilurus*.

3) Ribs and rib ligaments:

- Ribs:

In most squamates examined, the cervical ribs are unicipital and start on the fourth or fifth cervical vertebrae, but in *Sphenodon*, the first rib is bicipital and is on the third cervical vertebra. In *Caiman*, ribs are present on all cervical vertebrae (most intermediate muscles insert on the atlas rib), and the 2^{nd}-9^{th} ribs are short and bicipital (Hoffstetter and Gasc, 1969) (Table, 10.3.1) (plate, 10.3.9/a-b).

Except in those limbless forms (e.g. *Diplometopon* and *Trimeresurus*) where the pectoral girdle is reduced or absent, the cervical and dorsal ribs are connected to the pectoral girdle by short flat muscle slips. The origin of these and other muscles (e.g. iliocostalis major) from cervical ribs may be reflected by their wide or sometimes forked distal ends (e.g. gekkonids and cordylids) as well as by the presence of ridges and crests on the rib shafts. Rarely (*I. iguana*) there is a third cervical rib to atlas muscle, while *Diploglossus* and *Ophiodes* have muscle slips running between the cervical ribs and the intercentral apices. In limbless forms, such as *Diplometopon* and *Trimeresurus*, the dorsal and ventral processes

(pseudotuberculum) of the rib heads are connected to the vertebral body by short muscles.

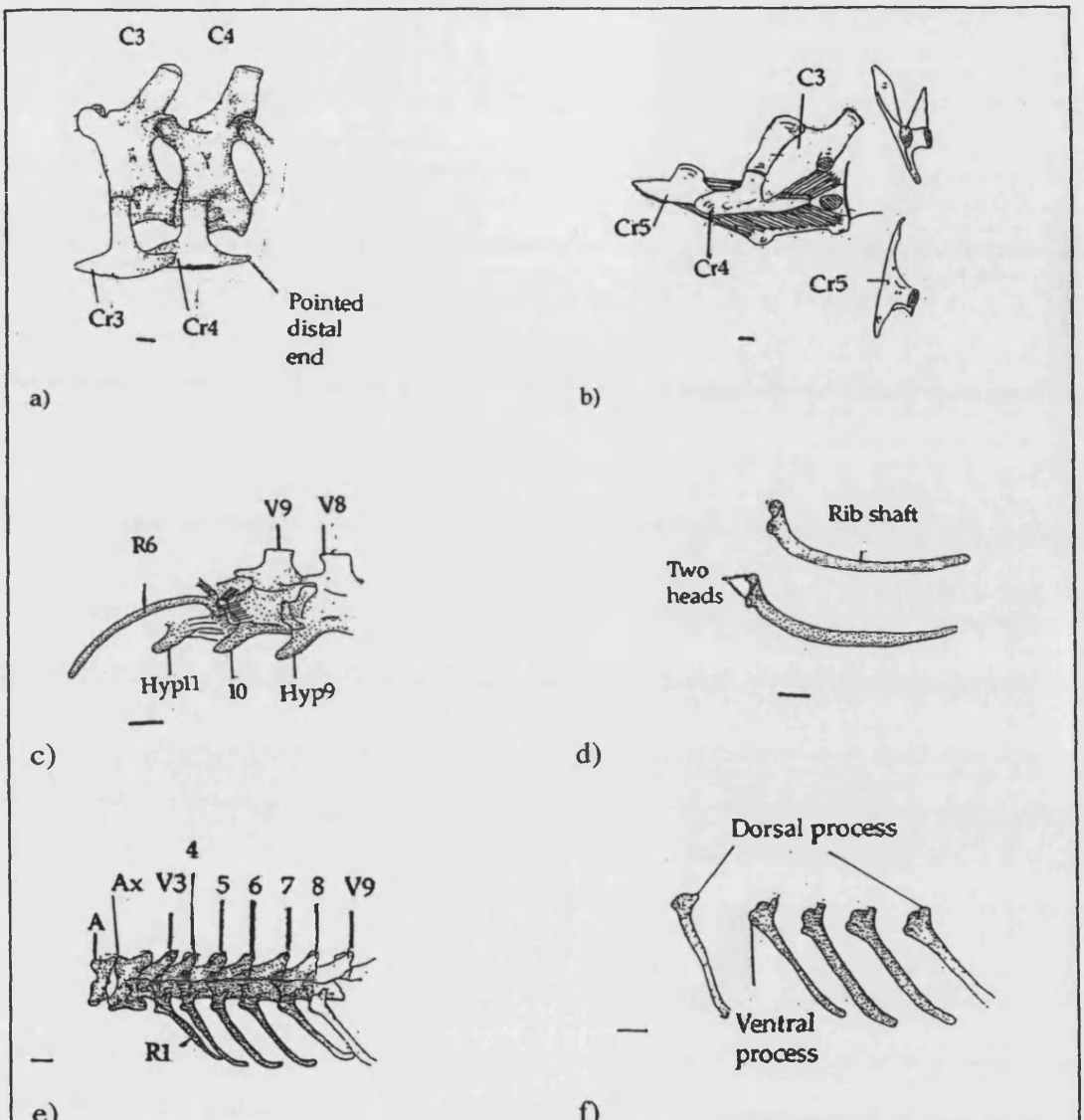


Fig. (10.3.9) a) *Crocodylus niloticus*, right lateral view of C3-4 with short Cr3-4 that are transverse with pointed distal ends.; b) *Caiman crocodilus*, right ventrolateral view of cervical vertebrae and the double-headed articulation of the cervical ribs (Cr); c) *Trimeresurus albolabris*, anterior lateral view of vertebrae 8-9 where rib articulates with the transverse process; d) *Trimeresurus albolabris*, anterior ribs with two costal processes (dorsal = ventral); e) *Trogonophis wiegmanni*, left lateral view of the cervical vertebrae where first rib articulates on vertebra 4; f) *Trogonophis wiegmanni*, anterior ribs with dorsal processes larger than the ventral processes. Scale bar = 1 mm.

These processes are either symmetrical (e.g., *Trimeresurus* [Fig., 10.3.9c-d]), or asymmetrical (e.g. *Trogonophis* – Fig., 10.3.9e-f). In chamaeleons, the

centra/intercentra give attachment to long muscle slips that insert on the adjacent rib shafts. Presumably this feature stabilises the neck.

There is thus a relationship between the shape of the cervical ribs and muscle attachments (pectoral girdle and iliocostalis major muscle slips), but this does not assist in the identification of the neck region. Limbless forms have short uniform ribs along the vertebral column.

- Rib ligaments:

In most lepidosaurs examined, the cervical and dorsal rib ligaments connect each rib to the adjacent transverse processes. However, in gekkotans and some scincomorphs, cervical ligaments attach instead to the intercentra (basal crests), while dorsal ligaments retain their connection to the transverse processes, especially after the last keeled intercentrum (where the trunk region begins) (see Fig., 10.3.3a). This feature can vary within families (e.g. *Scincus* v. *Tiliqua*; *Cordylus* v. *Gerrhosaurus*).

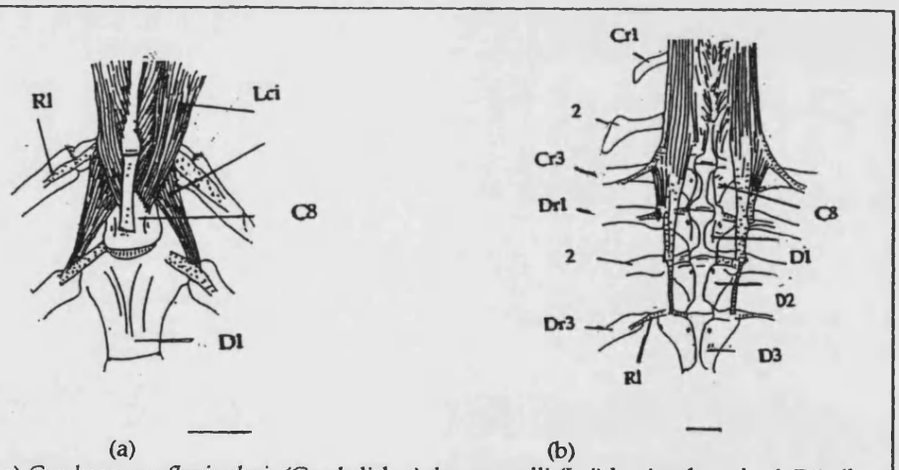


Fig. (10.3.10) a) *Gerrhosaurus flavigularis* (Cordylidae), longus colli (Lci) begins from both D1 rib ligament (Rl) (laterally) and C8 centrum (centrally); b) *Draco fimbriatus* (Agamidae*), longus colli (Lci) begins laterally from rib ligaments (Rl) (tendon) of dorsal vertebrae (D1-3). Scale bar = 1 mm.

In *Sphenodon* and most squamates examined, the longus colli and/or longus cervicus originate as slips from these rib ligaments regardless of ligament

attachment (centra or intercentra) (Fig., 10.3.10a-b). Although some taxa do show a change at the beginning of the dorsal region (e.g. gekkotans), the ventral muscles in limbless taxa (*Trimeresurus* and *Diplometopon*) originate from both centra and intercentra, and both the neck and trunk ligaments are short (attach to the transverse processes).

Basioccipital

The longus colli is an important and powerful hypaxial muscle of the neck, producing ventral flexion. In squamates, it inserts on the basal tubera of the basioccipital, whereas in *Caiman* the muscle divides anteriorly and makes an additional attachment to the paroccipital process (Fig., 10.3.11a).

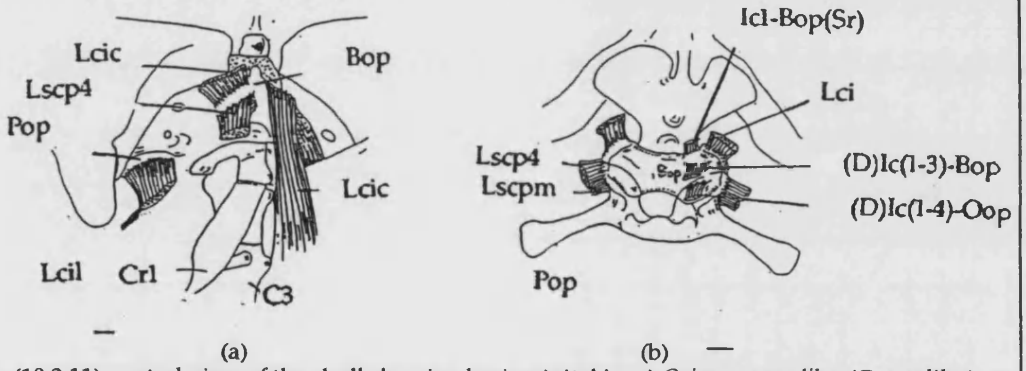


Fig. (10.3.11) ventral view of the skull showing basioccipital in, a) *Caiman crocodilus* (Crocodiles), where longus colli is divided to insert on basioccipital (Lcic) and oto-occipital (Lcil); b) *Lacerta trilineata* (Lacertidae), where most hypaxial muscles such as longus colli (Lci), intercentral muscle slips (Ic1-4) insert on the basioccipital (Bop) and oto-occipital (Oop). Scale bar = 1 mm.

In all taxa examined the first intercentral muscle slip inserts on the basioccipital, but in some groups (e.g. scincomorphs and iguanians) the muscle widens and extends its attachment to include oto-occipital (Fig., 10.3.11b). Posterior intercentral muscle slips occurred in all lepidosaurs examined, inserting on the basioccipital, the oto-occipital, or both. In most taxa, the first intercentral muscle slip inserts deep to longus colli, but in *Sphenodon*, most anguimorphs and

Trimeresurus it is completely covered by longus colli. Posterior intercentral muscle slips usually insert superficial and lateral to first intercentral muscle slip but in gekkotans, *Shinisaurus* and anguids they insert in a deeper position. In varanids and *Diplometopon* all the intercentral slips insert at the same level on the basioccipital and oto-occipital (Fig., 10.3.12).

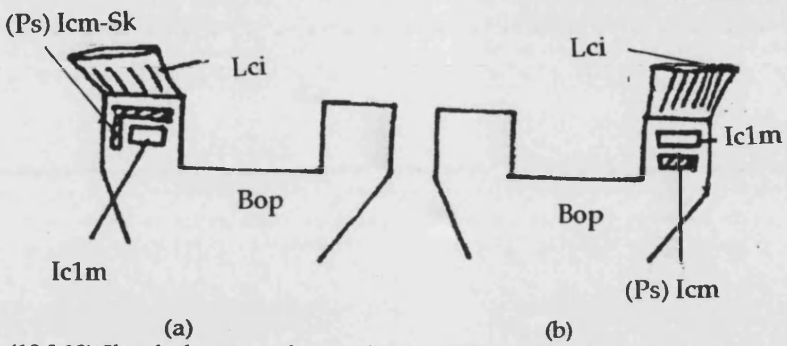


Fig (10.3.12) Sketch drawing of ventral view of the basioccipital (Bop) showing a) insertion of posterior intercentral muscle slips to skull ([Ps]Icm-Sk) superficial & lateral to first intercentral muscle slip (Ic1m) (most taxa); b) posterior intercentral muscle slips insert deep to first intercentral muscle slip (some taxa). Scale bar = 1 mm.

- Shape of the basal tubera:

The basal tubera may have oval, triangular or elongated epiphyses. In most lepidosaurs examined, the longus colli inserts as a straight thick muscle bundle, with or without a tendon, onto an oval or triangular epiphysis. The exceptions are varanids where the muscle inserts with a curved tendon and *Diplometopon* (basioccipital and oto-occipital) where it inserts as a flat bundle, leaving elongated epiphyses. In *Trimeresurus* and varanids uniquely, the longus colli runs on the anteromedial surface of the basioccipital, inserting centrally in the snake, but curving laterally as a tendinous bundle to insert on an elongated epiphysis in varanids. However, in many taxa, the shape of the basal tubera shows intraspecific and interspecific variation (e.g. the *Uromastyx* adult has oval tubera, but in the juvenile they are triangular; *Tiliqua rugosa* has elongated

tubera, while *Tiliqua nigrolutea* has oval tubera), and this reduces their general phylogenetic value.

Other muscles such as longissimus capitis 4 and the intercentral muscle slips may also play a part in shaping the basioccipital/oto-occipital. So while the presence of the basal tubera is directly related to the attachment of cervical muscles, the shape reflects individual age and size, as well as the number, thickness and mode of attachment of inserting muscles (Fig.10.3.13).

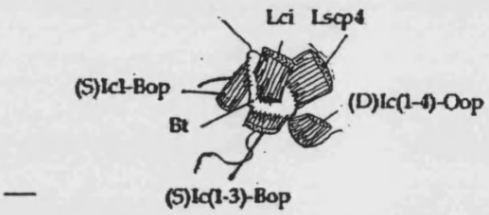


Fig. (10.3.13) *Iguana iguana*, ventral view of the basioccipital showing the left triangular basal tuberculum (Bt) where intercentral muscles to skull (Ic-Bop&Oop), longissimus capitis 4 (Lscp4) and longus colli (Lci) insert. Scale bar = 1 mm.

Oval	*Anolis biporcatus*; chamaeleons; *Uromastyx*-adult, *Moloch*; Gekkota; *Heloderma*; *Anguis, Ophiodes, Diploglossus; Tiliqua nigrolutea, Cordylus polyzonus, Pseudocordylus.*
Triangular	*Sphenodon; Anolis richardii, Anolis edwardii, Oplurus, Iguana, Crotaphytus, Phrynosoma; Uromastyx*-juvenile, *Calotes, Agama; Gerrhosaurus.*
Elongated	*Caiman; Phrynocephalus, Pogona; Scincus, Tiliqua rugosa*, lacertids, teiids; *Varanus, Shinisaurus, Elgaria; Diplometopon; Trimeresurus.*

(The different shape of the basal tubera in *Caiman* and examined lepidosaurs.)

- Presence or absence of a ridge between the two basal tubera:

The central area between the basal tubera is usually smooth, but may possess a linear ridge where the first intercentral (hypapophysis) muscle slip inserts, although the relationship is not simple (Fig., 10.3.11b). In *Anguis fragilis*, the ridge is longer and thicker because the first intercentral muscle slip and the clavicle to basioccipital muscle insert there.

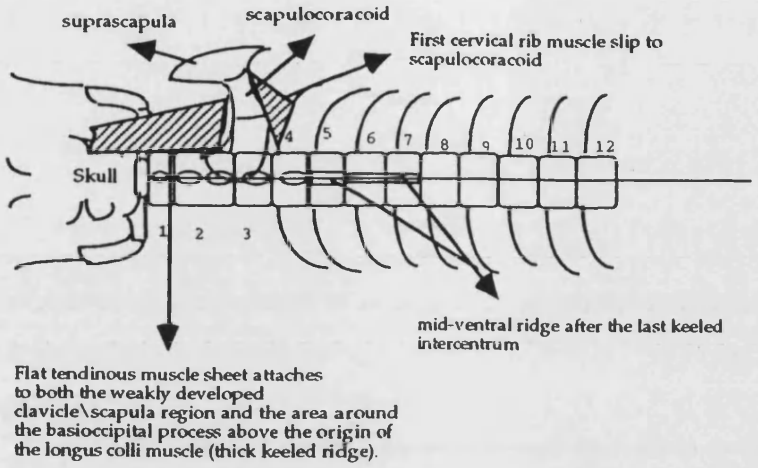


Diagram (10.3.2) ventral view of the craniocervical region showing the insertion of the clavicle to basioccipital muscle superficial to longus colli, leaving a thick keeled ridge between the basal tubera in *Anguis fragilis*.

In some taxa (e.g. *Diplometopon*) the area is smooth despite the attachment of the muscle, and the character also shows intraspecific variation in *Uromastyx*. This suggests that while the presence of the basioccipital ridge is directly related to the insertion of the first intercentral muscle slips, its prominence reflects age and body size, as well as muscle strength and use.

Summary

The above discussion makes it clear that the ventral part of the neck is distinguished by a number of specialised features which relate to muscle attachment:

1) The presence of the vertebral mid-ventral ridge correlates with the presence of the keeled intercentra (where ventral cervical muscles attach), and does not usually extend into the dorsal region (except *Ophiodes*). Moreover, the persistence of mid-ventral ridge on vertebrae behind the last keeled

intercentrum reflects the posterior extension of ventral cervical muscles, and may assist in the identification of the neck region.

2) There is a relationship between the presence, shape and size of keeled cervical intercentra and the presence, thickness and mode of attachment of ventral cervical muscles (e.g. longus colli, longus cervicus and intercentral muscle slips to the skull). However, since the ventral cervical muscles may extend back beyond the level of the last intercentrum, the last keeled intercentrum does not always mark the neck/trunk boundary (e.g. *Heloderma*). In snakes, hypapophyses persist after the cervical musculature has ended.

3) The presence of the intercentral lateral crests marks the attachment of longus cervicus, which is usually limited to the cervical region, while the presence of the basal crests reflects the attachment of rib ligaments, which occur on both cervical and dorsal regions.

4) The size of the rib ligaments (long or short), or their attachment position (centra or intercentra) may differ between cervical and trunk region (e.g. gekkotans), but does not vary in snakes and amphisbaenians.

5) The morphology of the anterior ribs (e.g. wide or forked) reflects muscle attachment (mainly of pectoral girdle muscle slips), but there is no variation in snakes and amphisbaenians.

6) Ventral axial muscles (e.g. longus colli) that originate from the presacral vertebral column insert on the basioccipital. The size and the thickness of the hypaxial muscles influences the shape and surface morphology of the basisphenoid.

Table (10.3a) Osteology of the ventral side of the cervical vertebrae

Genus	No. of cervical vertebrae	No. of cervical ribs	Rib ratio	Rib ligaments	No. of cervical intercentra	No. of keeled intercentra	No. of intercentral muscles
Caiman	9	9	-	-	12	11	1
Sphenodon	8	6	2+1+4+1	Present	9	7	2
Iguanidae*	8	4	4+2+2	Present	5	5	4
Anolis							
Iguana	8	4	4+2+2	Present	5	5	5
Oplurus	8	4	4+2+2	Present	6	6	5
Crotaphytus	8	5	3+3+2	Present	6	6	5
Phrynosoma	8	5	3+3+2	Present	5	6	5
Agamidae*	8	4	4+2+2	Present	4-6	4-6	3
Uromastyx							
Ceratophora	8	5	3+3+2	Present	5	5	4
Moloch	8	4	4+2+2	Present	2	2	2
Draco	8	3	5+3	Present	7	7	6
Calotes	8	4	4+2+2	Present	6	6	2
Phrynocephalus	8	4	4+2+2	Present	6	6	4
Agama	8	4	4+2+2	Present	6	6	3
Pogona	8	4	4+2+2	Present	6	6	4
Chamaeleonidae	5	2	3+2	-	5	5	5
C. chamaeleon							
C. jacksonii	5	2	3+2	-	2	2	2
C. vulgaris	5	2	3+2	-	3	3	3
C. dilepis	5	2	3+2	-	4	4	4
Gekkota	8	5	3+3+2	Present	8	8	3
Hemidactylus	8	5	3+3+2	Present	8	8	1
Tarentola							
Phelsuma	8	5	3+3+2	Present	8	8	2
Gekko	8	5	3+3+2	Present	7-8	7-8	3
Chondrodactylus	8	5	3+3+2	Present	8	8	3
Ptychozoon	8	5	3+3+2	Present	8	8	3
Uroplatus	8	6	2+4+2	Present	4-5	4-5	4
Eublepharis	8	5	3+3+2	Present	5-7	5-7	2

Scincidae *Scincus* *Tiliqua*	8	5	3+3+2	Present	6-7	6-7	3
	8	5	3+3+2	Present	7	7	3
Cordylidae *Cordylus* *Gerrhosaurus*	8	5	3+3+2	Present	4-5	4-5	4
	8	5	3+3+2	Present	5	5	3-4
Lacertidae *Lacerta* *Acanthodactylus*	8	5	3+3+2	Present	7-8	7-8	4
	8	5	3+3+2	Present	5-6	5-6	4
Teiidae *Ameiva* *Kentropyx*	8	5	3+3+2	Present	6	6	5
	8	5	3+3+2	Present	6	6	5
Anguidae *Elgaria* *Diploglossus*	8	5	3+3+2	?	5	5	4
	8	5	3+3+2	?	7	7	4
Ophiodes	6	3	3+2+1	Present	6	6	5
Anguis	8	–	1st rib on vertebra 4	?	5	5	4
Xenosauridae *Shinisaurus*	8	5	3+3+2	Present	5	5	3
Helodermatidae *Heloderma*	8	5	3+3+2	Present	4	3	2
Varanidae *Varanus*	9	3-4	5+2+2	Present	9-10	9-10	3-4
Diplometopon	Not-differentiated	1st rib on vertebra 4	-	Present	10	10	10
Trimeresurus	Not-differentiated	1st rib on vertebra 4	-	Present	Continue along vertebral column	Continue along vertebral column	6

- Most lepidosaurs examined retain 8 cervical vertebrae.
- All lepidosaurs examined possess rib ligaments (except *Sphenodon* and *Chamaeleo*).
- The number of intercentra is variable (2-10), in *Trimeresurus* and many gekkotans + *Sphenodon* they continue posteriorly.
- Usually, all intercentra are keeled.
- The number of keeled intercentra does not match the number of intercentral muscle slips to the skull except in *Diplometopon* (10), *Iguana* (5), *Moloch* (2) and *Chamaeleo* (2-5).

Table (10.3b) Origin, insertion and mode of extension of longus colli and cervicus muscles

	Longus colli			Longus cervicus		
	First origin	Mode of extension	Final insertion	First origin	Mode of extension	Final insertion
Caiman	D5	2 bundles	Basioccipital + paroccipital	Absent		
Sphenodon	D2-3	3 bundles	Basioccipital	D4-5	2 bundles	2nd + 3rd intercentra
Anolis	D1	2 bundles	"	C8	1 bundle	2nd intercentrum
Iguana	C7	"	"	C7	"	"
Oplurus	D1	"	"	C8	"	"
Crotaphytus	D1	"	"	D1	"	"
Phrynosoma	D3	"	"	D2	"	"
Uromastyx	C8	"	"	C6	"	"
Ceratophora	D1	"	"	C7	"	"
Moloch	D3	"	"	D2	"	"
Draco	D3	"	"	D2	"	"
Calotes	D1	"	"	D1	"	"
Phrynocephalus	C8	"	"	C8	"	"
Agama	D2	"	"	D2	"	"
Pogona	D2	"	"	D2	"	"
C. chamaeleon	D3	1 bundle	"	Absent		
C. jacksonii	D2	"	"			
C. vulgaris	D3	"	"			
C. dilepis	D2	"	"			
Hemidactylus	C8-D	"	"	C8-D1	2 bundles	2nd + 3rd intercentra
Tarentola	"	"	"	"	"	"
Phelsuma	"	"	"	C7-8	"	"
Gekko	"	"	"	"	"	"
Chondrodactylus	"	"	"	C8-D1	"	"
Ptychozoon	"	"	"	C7-8	"	"

Uroplatus	D1-2	"	"	D1-2	"	"
Eublepharus	C7	"	"	C7	"	"
Scincus	D3	3 bundle	"	C7	1 bundle	2nd intercentrum
Tiliqua	D1-2	1 bundle	"	C7	"	"
Cordylus	C8	"	"	C6	"	"
Gerrhosaurus	D1	"	"	C7	"	"
Lacerta	D1	"	"	C8	"	"
Acanthodactylus	C8	"	"	C6	"	"
Ameiva	D1	"	"	C6	"	"
Kentropyx	D1	"	"	C8	"	"
Elgaria	C8	"	"	C5 reduced	"	4th intercentrum
Diploglossus	D2	"	"	C8	3 bundles	2nd intercentrum
Ophiodes	D3	"	"	C6	1 bundle	"
Anguis	C8	"	"	Absent		
Shinisaurus	C8	3 bundles	"	C5 reduced	3 bundles	3rd+4th+5th centra
Heloderma	C8	1 bundle	"	C8	Short muscle slips (reduced)	3rd-4th intercentra & 4th-5th centra
Varanus	C6	"	"	D2 reduced	Long tendons (reduced)	2nd intercentrum
Diplometopon	V 21	"	basioccipital & exoccipital	Vertebra 7 reduced	One thin tendon	"
Trimeresurus	V 9	"	basioccipital	Absent		

4- The atlas-axis complex

In amniotes, movement of the head is facilitated by the development of an elongated neck and the modification of the first two vertebrae into a specialised craniocervical joint (Romer, 1956). The atlas is the first vertebra and articulates with the condyle (s) of the skull; the axis articulates normally with the remaining cervical vertebrae and forms a pivot where the atlas vertebra turns (Webb et al., 1978).

Osteology of the atlas-axis complex

Anterior to the atlas arch in some taxa lies the proatlas component (Albrecht, 1883), which forms a small paired structure shaped like an inverted V, obscured between the skull and the atlas. This element is reported in most early amniotes (Osborn, 1900; Romer, 1956; Hoffstetter and Gasc, 1969; Carroll; 1970; Young, 1981) and also in crocodiles, *Sphenodon* and, reportedly, chamaeleons (Romer, 1956), but I did not see a proatlas in chamaeleons

The atlas is formed by a pair of dorsal, half-arch structures that articulate ventrally with a broad intercentrum (except in advanced snakes = complete ring, Romer, 1956). The atlas intercentrum bears a ventral projection, which is deep in most squamates (except helodermatids), but flat in *Caiman* and *Sphenodon*. In squamates, the atlas arch usually remains separate from the axis (no atlantal postzygapophyses), but the atlas still articulates ventrally with the anterior odontoid process of the axis (= first centrum). In chelonians and crocodilians the atlas has postzygapophyses which articulate with the prezygapophyses of the axis, and this condition is found in very primitive lepidosaurs – e.g. the primitive

rhynchocephalian *Gephyrosaurus* (Evans, 1981). Paranjape (1974) suggested that the anterolateral tuberosities (transverse processes) of the atlas and axis in reptiles might also assist their articulation. In crocodiles, the first rib articulates with the atlas intercentrum (Hoffstetter and Gasc, 1969), and the second rib with the fused odontoid (i.e. the axis centrum bears no ribs). The axis in lepidosaurs is a compound vertebra with a well-developed wide neural arch, an elongated centrum that bears the odontoid, and one or two modified intercentra.

Myology of the atlas-axis complex

Several muscles connect the atlas and axis to one another, to the skull, or to the rest of presacral vertebral column.

1) Muscles between the atlas and axis complex

In most reptiles, the principal atlantoaxial joint is that between the atlas intercentrum and the odontoid process of the axis. In Lepidosauria generally, a short thick epaxial muscle originates from the neural spine/arch of the axis (biconcave surface), and converges to insert on the posterior side of the atlantal arch (curved groove). Laterally, there are two slips - the dorsal longissimus cervicus and the ventral iliocostalis cervicus, which insert on the atlas, such that, with some exceptions, the former slip inserts on the posterior process, and the latter on the transverse process (Fig., 10.4.1a). However, in *Sphenodon*, the longissimus cervicus branches anteriorly to insert additionally on the proatlas, while in the iguanian *Phrynosoma*, the iliocostalis cervicus branches to insert as a pair of tendons

on the transverse process (Fig., 10.4.1b). In *Caiman*, the first rib is on the atlas and most of the muscles insert or originate from that rib (for example, episternocleidomastoid, iliocostalis cervicus and levator scapulae dorsalis and ventralis).

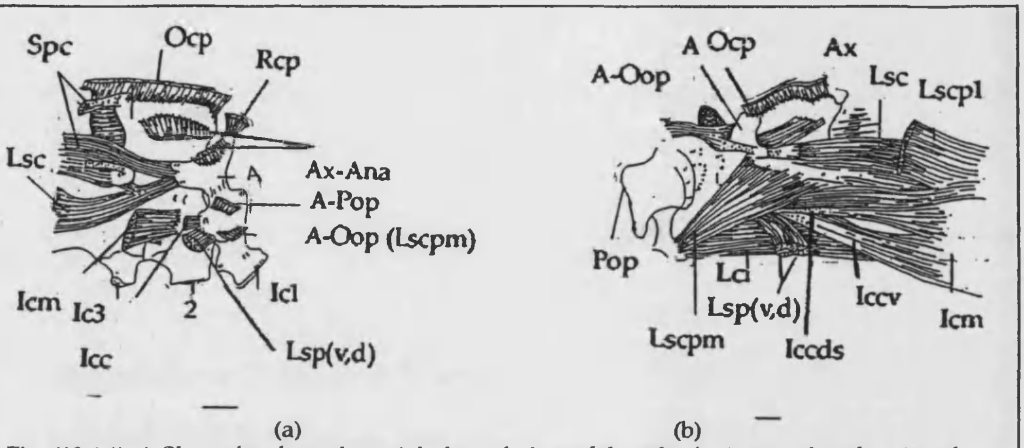


Fig. (10.4.1) a) *Chamaeleo chamaeleon*, right lateral view of the atlas/axis complex showing the lateral insertion of longissimus cervicus (Lsc) on the posterior process of the atlas and the iliocostalis cervicus (Icc) on transverse process, also the axis to atlas neural arch muscle (Ax-Ana); b) *Phrynosoma platyrhinos*, left lateral view of the atlas/axis complex showing the division of the iliocostalis cervicus into iliocostalis cervicus ventralis (Iccv) and iliocostalis cervicus dorsalis (Iccds). Scale bar = 1 mm.

2) Muscles between atlas/axis complex and skull

In lepidosaurs generally, the complex is connected to the cranium through several short muscles, but in *Sphenodon* the proatlas is located anterior to the complex and is linked to the exoccipital by a tendinous bundle. In most lepidosaurs examined, the short dorsal rectus and obliquus capitis join both neural arches of the complex to the skull. In *Caiman*, chamaeleons and gekkonids both muscles originate from the anterior cervical spines, while in *Caiman*, *Scincus* and *Gerrhosaurus* obliquus capitis additionally originates from the posterior cervical spines (plate, 10.4.2a). In some taxa, the obliquus and rectus capitis are also sub-divided into superficial and deep layers. This elongation and division may assist mobility of the craniocervical region rather than simply fixing the complex to the skull. In

all squamates, the atlantal arches also give an attachment to a short deep muscle (atlas to skull) which runs (under rectus capitis) to the supraoccipital/exoccipital (e.g. *Scincus*) (Fig., 10.4.2b). Other epaxial muscles such as spinalis capitis originate from the posterior cervical spines (except in *Uroplatus* [axis] and Varanidae [C2-4]), and insert on the parietal. In *Sphenodon*, an extra short muscle slip begins from the axis neural spine to insert on the supraoccipital (median crest). Longissimus capitis 3 is absent in *Caiman* and most lepidosaurs, but is present in *Sphenodon*, *Iguana* and chamaeleons. In *Sphenodon*, the muscle branches from the longissimus dorsi at the level of the axis centrum (small crest). Longissimus capitis minor usually branches from the atlas posterior process (at the insertion of longissimus cervicus), but in Chamaeleonidae, it originates more anteriorly leaving a shallow ridge on the anterior side of the atlas transverse process. Furthermore, the atlas in Chamaeleonidae has an additional short muscle slip that originates dorsal to longissimus capitis minor and inserts on the paroccipital process (atlas to paroccipital process [A-Pop]; see Fig., 10.4.1a).

Ventrally, a series of muscles run from the intercentral complex of the atlas-axis to the basicranium (basioccipital + sphenoid). The atlantal intercentral muscle usually inserts as a single layer on the basioccipital, except in Iguania and Scincomorpha where it is thicker and divided into superficial (basioccipital) and deep (basioccipital and oto-occipital) layers. The second intercentral muscle slip usually originates from the anterior axis intercentrum (second intercentrum) which is keeled, but in *Sphenodon* and *Heloderma*, this muscle slip is absent and the intercentrum is flat.

Where present, the third intercentral muscle slip to the skull originates from the posterior axis intercentrum (third intercentrum), which is also keeled. The intercentrum may be sutured (e.g. *Sphenodon* and Gekkota) or fused (Scincomorpha and Anguimorpha) to the axis or cervical 3.

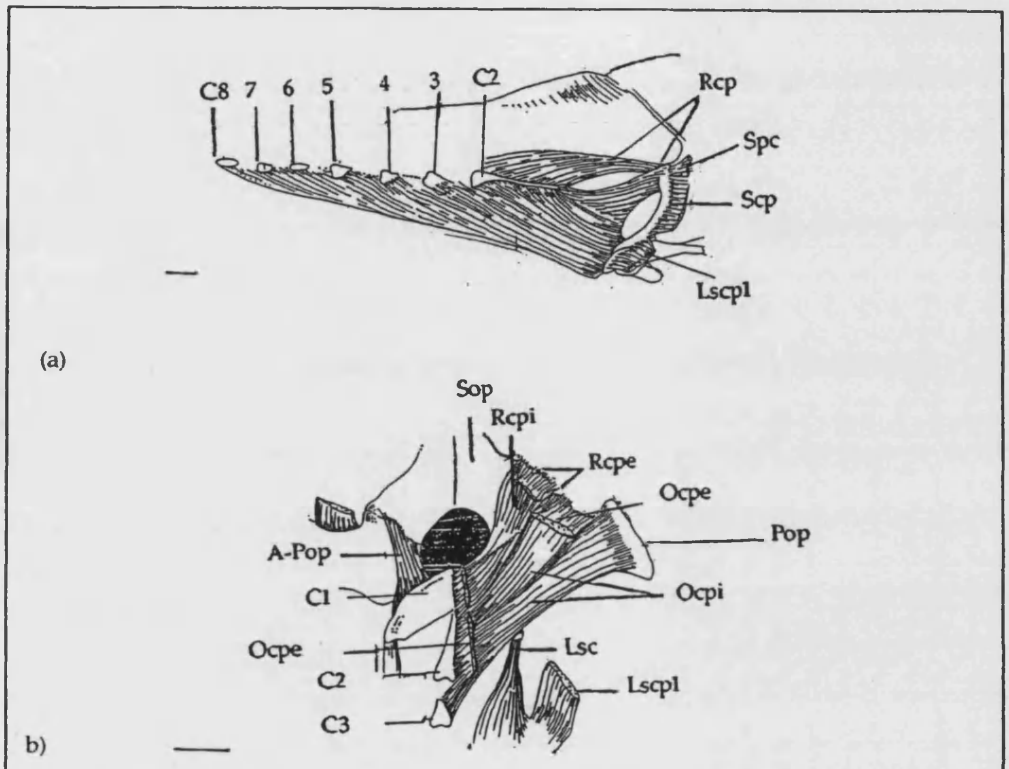


Fig. (10.4.2) *Scincus miternus*, a) right dorsal view of the craniocervical region showing the posterior origin of obliquus capitis (Ocp) from C2-8; b) dorsal view of the atlas/axis complex showing the sub-division of obliquus capitis into externus and internus (Ocpe &Ocpi), and rectus capitis internus and externus (Rcpe & Rcpi), also shows the atlas to supraoccipital muscle (A-Pop). Scale bar = 1 mm.

3) Muscles between the atlas/axis complex and the presacral vertebral column and pectoral girdle

There are a number of intermediate and deep muscles that originate posteriorly and run forward to insert on the atlas and axis. Dorsally, the spinalis cervicus muscle inserts on the posterodorsal process of the axis (triangular/oval shape), while the spinalis/semispinalis cervicus muscle slips attach on small tubercles on the axial postzygapophyses

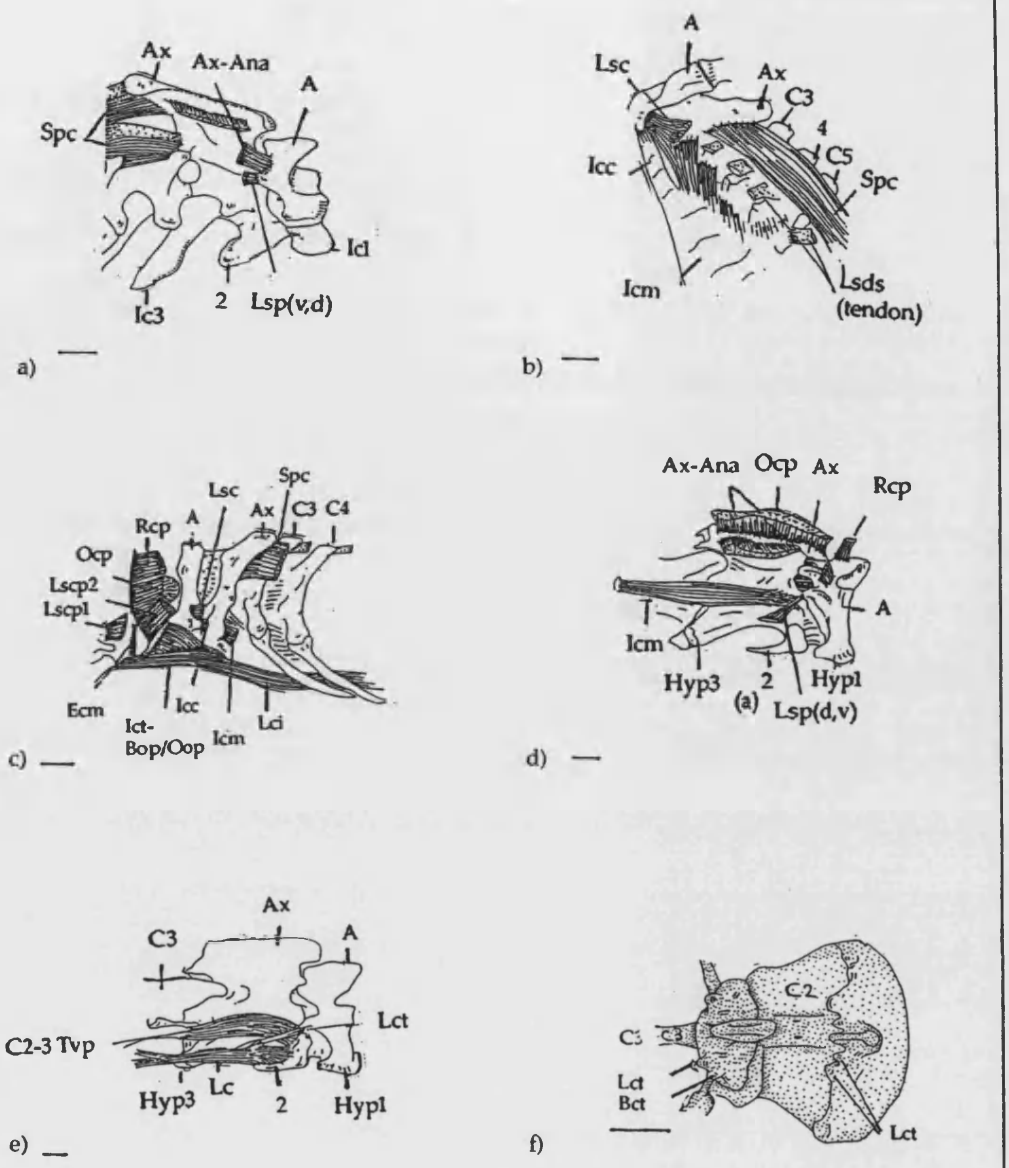


Fig. (10.4.3) a) *Scincus miternus*, right lateral view of the atlas/axis complex showing the insertion of the spinalis cervicus (Spc) on the axis neural spine and arch. b) *Diplometopon zarudnyi* left dorsal view of the anterior vertebrae showing the atlas/axis complex with spinalis cervicus (Spc) inserting on the axis neural spine and arch. c) *Diplometopon zarudnyi*, left lateral view of the anterior vertebrae showing the attachment of iliocostalis cervicus (Icc). d) *Varanus griseus*, right lateral view of the atlas/axis complex showing the insertion of axis to atlas muscle (Ax-Ana), and iliocostalis major (Icm). e) *Varanus griseus*, right lateral view of the atlas/axis complex showing the lateral crests (Lct) under the atlas transverse process (Tvp) where longus cervicus (Lc) has a V - shaped insertion. f) *Gekko gecko*, ventral view of the axis showing the double lateral crests (Lct) where longissimus cervicus inserts on the axis first intercentrum and basal & lateral crests (Bct & Lct) on the axis second intercentrum where rib ligaments & longissimus cervicus inserts. Scale bar = 1 mm.

(Fig., 10.4.3/a-b). Laterally, longissimus cervicus branches from longissimus dorsi along the axis postzygapophyses to insert on the atlas posterior processes (see Fig., 10.4.1a – 10.4.2b). *Caiman* is the only taxon

examined which retains a rib on the atlas. This rib gives attachment to muscles connecting the cervical vertebral column, the pectoral girdle (levator scapula dorsalis/ventralis and the episternocleidomastoid) and the posterior ribs (iliocostalis cervicus).

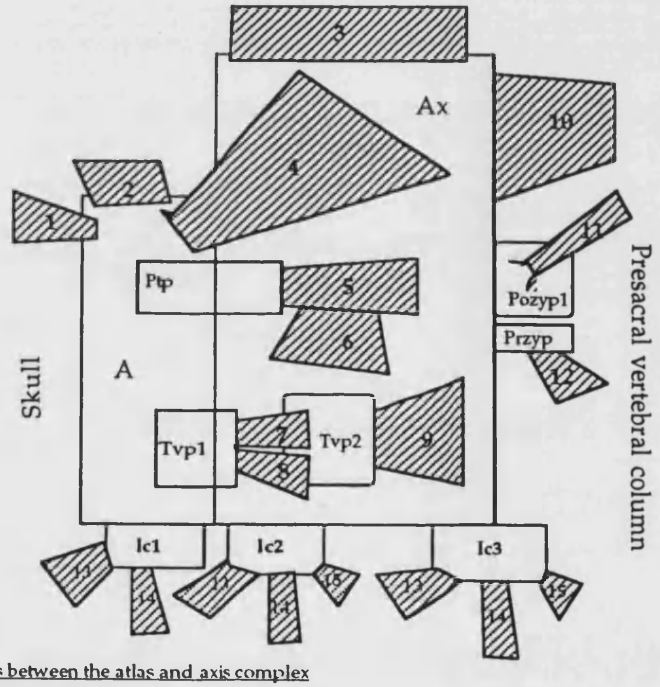
In Lepidosauria, the same muscles attach instead to the atlas transverse process (leaving small grooves where iliocostalis cervicus attaches), and to the skull (changing the thickness of the distal end of the paroccipital process and resulting in the development of epiphyses) (Fig., 10.4.3c-d). Attachment to the skull may improve control of head movement. As noted above, in some squamates examined the posterior intercentra had lateral and basal crests (where longus cervicus slips and rib ligaments end). The longus cervicus in all taxa examined terminates on the anterior intercentrum of the axis (usually pointed posteriorly and sometimes with lateral crests), but another slip of the longus cervicus muscle (or its tendon) attaches to the posterior axial intercentrum (smooth or with lateral crests) (Fig., 10.4.3e). Gekkota is the only lizard group with double lateral crests on the anterior and posterior axis intercentra (Fig. 10.4.3f).

This reflects the division of longus cervicus into superficial and deep parts. In some anguids (e.g. *Ophiodes* and *Diploglossus*), a narrow tendinous muscle extends along longus colli and connects the first or second intercentrum to the suprascapula.

Summary

In reptiles, the atlas and axis are the first vertebrae of the neck, although in *Sphenodon* a tiny proatlas remains between the atlas and skull. The proatlas attaches to the vertebral column by the anterior branch of the longissimus

cervicus, and to the skull by a tendinous sheet. The atlas and axis are highly modified and functionally distinct from other cervical vertebrae. In squamates, the articulation between the atlas and axis neural arch (zygapophyses) is lost, leaving only the articulation between the atlas and the odontoid process (usually ball and socket), although there are epaxial and hypaxial muscle slips that link various parts of the complex. This reduced stability in squamates may be compensated for by the thicker axis – atlas muscle slip. The muscles assist in fixing the skull (e.g. chamaeleons [large skull] = extra atlas to oto-occipital muscles) and allow movement of the craniocervical region.



Muscles between the atlas and axis complex

4- Axis to atlas muscle

Muscles between atlas/axis complex and skull

1- Atlas to paroccipital process
2- Rectus capitis
3- Obliquus capitis
6- Longissimus capitis minor
13- Intercentra to basioccipital/oto-occipital
14- Longus colli

Muscles between atlas/axis complex and presacral vertebral column and pectoral girdle

5- Longissimus cervicus
7- Levator scapula dorsalis
8- Levator scapula ventralis
9- Iliocostalis major
10, 11- Splenius cervicus and /spinalis cervicus
12- Longissim dorsi
15- Longus cervicus

Diagram (10.4.1) left lateral view showing the atlas/ axis muscle complex.

5- The pectoral girdle and sternum

In primitive amniotes the pectoral girdle consists of the clavicle, interclavicle, sternum, scapulocoracoid and cleithrum, but the latter is lost in living amniotes (Romer, 1956; Carroll, 1988). In modern tetrapods, muscles connect the pectoral girdle to the vertebral column. Zaaf et al. (1999) related the morphology of the appendicular musculature to different types of locomotion. For example, the climber *Gekko gecko* has more powerful retractor muscles in the pectoral and pelvic girdles than the ground running *Eublepharis macularis*.

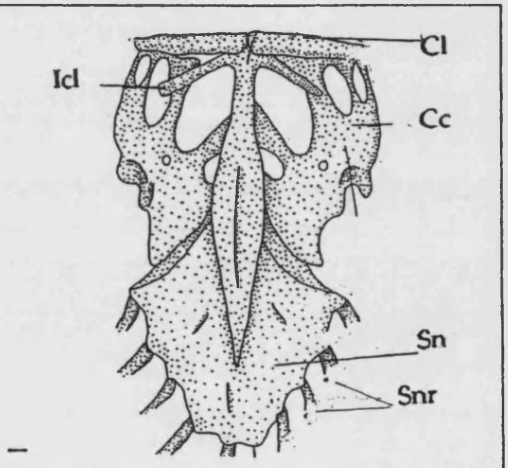


Fig. (10.5.1) *Iguana iguana*, ventral view of the pectoral girdle showing the clavicle (Cl), interclavicle (Icl), coracoid (Cc) and sternum (Sn). Scale bar = 1 mm.

The scapulocoracoid consists of the scapula and its dorsal cartilaginous suprascapula, and the ventral coracoid (Fig. 10.5.1). Between them they form the glenoid articulation for the head of the humerus. Besides these, there are the clavicles, the median interclavicle, and the cartilaginous sternum. The clavicle is present in most squamates even if the forelimbs are absent (e.g. pygopodids – Underwood, 1957), thus its absence is a derived feature (Evans and Barbadillo, 1997). It is a simple rod, which

develops an expanded perforated medial end in many groups (e.g. geckos). In *Caiman*, chamaeleons (where the interclavicle is lost in post-embryonic life [Lécuru, 1968; Skinner, 1959]), snakes (Bellairs and Underwood, 1951), and dibamids (Greer, 1985), the clavicle is lost. The interclavicle is primitively T-shaped (e.g. *Sphenodon*, iguanids), but becomes cruciform in many lizards (agamids, gekkotans; scincomorphs). The presence or absence of the interclavicle is linked to the reduction of the pectoral girdle overall or to functional reasons such as arboreality in Chamaeleonidae (Estes et al., 1988). Chamaeleons have a special compressed body shape, which is reflected in both limb girdles (Peterson, 1973; Gasc, 1981).

The contact between the coracoid and the sternum is movable to allow scapulocoracoid and glenoid to rotate in a horizontal plane (Bellairs, 1969). The position of the pectoral girdle is also related to neck length, especially in limbless lizards where the heart and the vestigial girdle are close to the head because the neck remains short (e.g. some limbless anguids).

In all lepidosaurs, the pectoral girdle has superficial, intermediate and deep muscles that connect the girdle to the dorsal muscle fascia, the skull, the cervical vertebrae and the ribs.

1) Muscles between the pectoral girdle and neural spines and muscle fascia

The trapezius is a superficial muscle that usually originates from the vertebral neural spines, but in *Sphenodon*, Chamaeleonidae and some iguanids it originates from the muscle fascia of splenius capitis. The muscle fibres converge to insert on the pectoral girdle (scapula, suprascapula, clavicle). Latissimus dorsi originates further posteriorly, also

from vertebral neural spines, to insert on the posterior margin of the humeral head.

2) Muscles between the pectoral girdle and the skull

The episternocleidomastoid and the clavicle dorsalis run together to link the clavicle/interclavicle with the occipital surface of the skull. The episternocleidomastoid inserts dorsally on the skull in lepidosaurs but in *Caiman* it ends on the atlas rib. Since it also inserts on the skull in mammals, the condition in *Caiman* may be derived. The clavicle dorsalis inserts on the skull and muscle fascia of splenius capitis or the muscle fascia only. It is absent in *Caiman*, Chamaeleonidae, most Anguimorpha, *Diplometopon* and *Trimeresurus*, but in *Anguis* may be represented by a short tendinous muscle that originates from the clavicle and inserts on the basioccipital (Fig., 10.5.2).

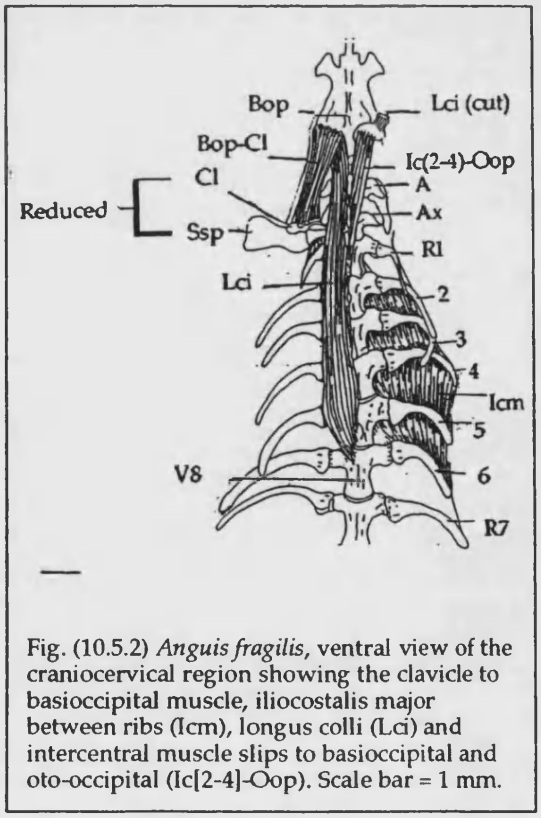


Fig. (10.5.2) *Anguis fragilis*, ventral view of the craniocervical region showing the clavicle to basioccipital muscle, iliocostalis major between ribs (Icm), longus colli (Lci) and intercentral muscle slips to basioccipital and oto-occipital (Ic[2-4]-Oop). Scale bar = 1 mm.

3) Muscles between the pectoral girdle and cervical vertebrae

The levator scapula dorsalis and ventralis were present in all taxa examined. They originate laterally from the atlas transverse process and run posteriorly as one long wide muscle to insert on the suprascapula. In some Anguidae (*Diploglossus* and *Ophiodes*) and Varanidae, however, there are additional muscles running from the intercentra to the pectoral girdle. In *Diploglossus* and *Ophiodes*, the intercentral muscle slips originate from the first or second intercentral apex (as a tendon), and extend posteriorly along the longus colli, becoming muscular, to insert on the suprascapula (Fig., 10.5.3a-c).

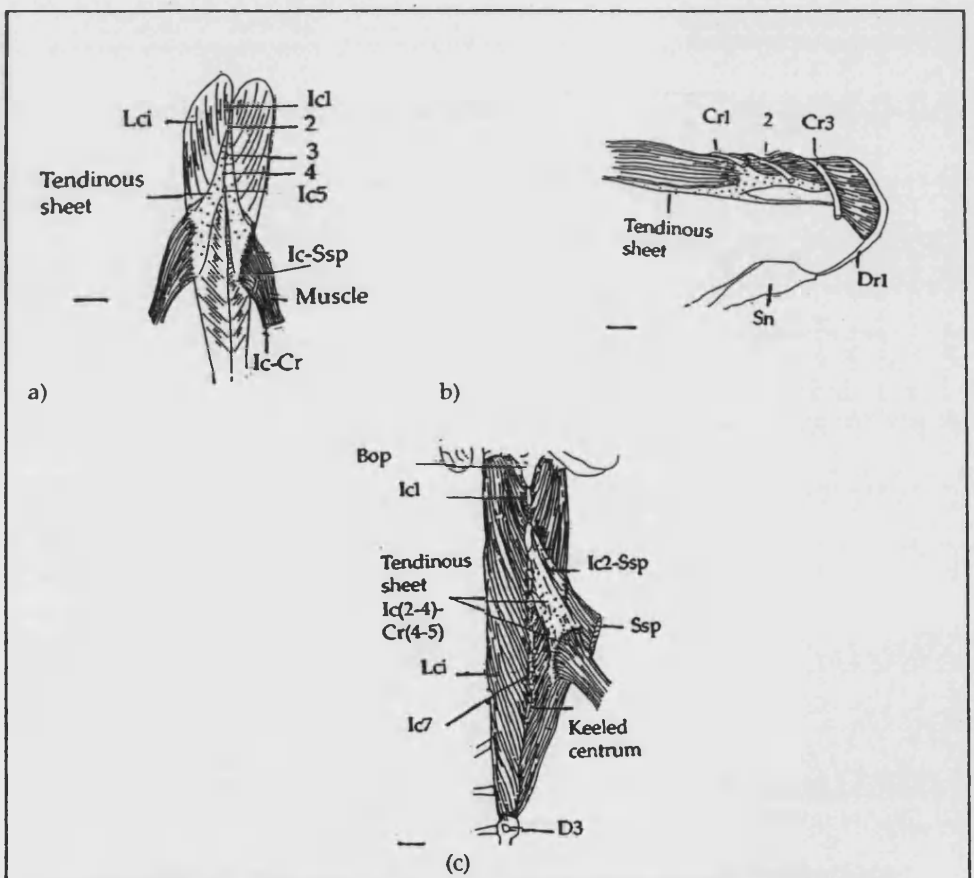


Fig. (10.5.3) *Ophiodes intermedius*, ventral view of the craniocervical region where an intercentral tendinous muscle inserts on the suprascapula and cervical ribs. b) *Ophiodes intermedius*, left ventral view of the pectoral girdle, ribs and sternum showing the extension and insertion of the intercentral tendinous sheet on 3rd cervical rib. c) *Diploglossus crusculus crusculus*, ventral view of the craniocervical region showing the intercentral tendinous muscle sheets to suprascapula and cervical ribs. Scale bar = 1 mm.

In varanids, there are two layers of intercentral (hypapophyseal) muscle sheets, originating from the specialized distal hypapophyseal epiphyses and inserting on the pectoral girdle. The more superficial hypapophyseal (4-7) muscular sheet inserts on the scapulocoracoid and clavicle, while the deeper hypapophyseal (4-6) muscular sheet ends on the suprascapula. These two muscle sheets were absent in all other taxa examined.

4) Muscles between the pectoral girdle and ribs (serratus muscles)

There are series of superficial anterior, middle and posterior muscle slips that originate from the distal end of cervical and dorsal ribs to insert on the suprascapula and scapulocoracoid. Those slips persist in *Caiman* where the clavicle is absent, in chamaeleons where clavicle and interclavicle are absent, and in the limbless *Anguis fragilis* where the interclavicle is absent. This observation agrees with Camp (1923) who argued that muscle attachment persists although some pectoral girdle elements are reduced. However, this is not the case in *Diplometopon* where the muscle slips from the ribs to the pectoral girdle are absent, despite the retention of rudimentary girdles, or in *Trimeresurus* (pectoral girdle absent).

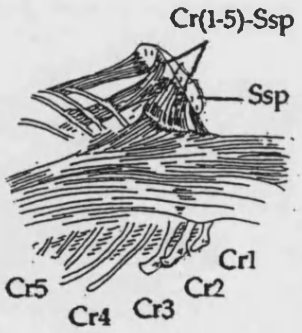


Fig. (10.5.4) *Tarentola mauritanica*, right dorsal view of the craniocervical region showing superficial muscle slips between ribs and pectoral girdle (Cr(1-5)-Ssp) and the forked distal ends of the cervical ribs (Cr2-3). Scale bar = 1 mm.

After removing the superficial serratus slips of cervical ribs a set of deep muscle slips appear, originating from the cervical ribs and inserting deep on the suprascapula. The forked distal ends of the cervical ribs in some scincomorphs (scincids and cordylids) reflect the attachment of the deep and superficial slips, as well as the iliocostalis major. The deep slips are absent in gekkotans, although the cervical ribs are still wide or forked, and the character shows intraspecific variation (e.g. *Gerrhosaurus flavigularis*).

Summary

The pectoral girdle is connected to the skull and presacral vertebral column by superficial and intermediate muscles. The most interesting slips are the unique hypapophyses to clavicle, scapulacoracoid and suprascapula slips in varanids, and the intercentra to suprascapula in some anguids. In some taxa (e.g. some cordylids), the thickness and division of the muscle slips may affect the shape of the distal ends of the cervical ribs, but other muscles also play a role. In some gekkotans, the distal ends of the cervical ribs are forked despite the absence of deep slips. This needs further investigation.

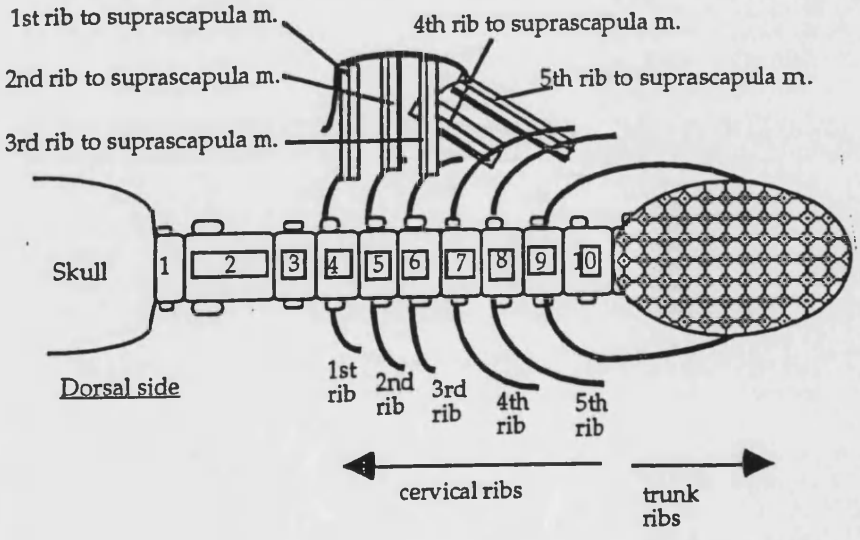


Diagram (10.5.1) dorsal aspect of the craniocervical region in *Elgaria* (anguid) with cervical vertebrae, and rib muscle slips to suprascapula.

Table (10.5) Osteology of the pectoral girdle in reptiles

Genus	Pectoral girdle			
	Clavicle	Interclavicle	Scapulocoracoid	Suprascapula
Caiman	Absent	Well-developed		
Sphenodon	Well-developed			
Iguanidae* *Anolis* *Iguana* *Oplurus* *Crotaphytus* *Phrynosoma*	Well-developed			
Agamidae* *Uromastyx* *Ceratophora* *Moloch* *Draco* *Calotes* *Phrynocephalus* *Agama* *Pogona*	Well-developed			
Chamaeleonidae *C chamaeleon* *C. jacksonii* *C. vulgaris* *C. dilepis*	Absent	Absent	Narrow	Short & wide
Gekkonidae *Hemidactylus* *Tarentola* *Phelsuma* *Gekko* *Chondrodactylus* *Ptychozoon* *Uroplatus*	Well-developed			
Eublepharidae	Well-developed			
Scincidae *Scincus* *Tiliqua*	Well-developed			
Cordylidae *Cordylus* *Gerrhosaurus*	Well-developed			
Lacertidae *Lacerta* *Acanthodactylus*	Well-developed			
Teiidae *Ameiva* *Kentropyx*	Well-developed			

<table>
<tr><td rowspan="3">Anguidae
Elgaria
Diploglossus
Ophiodes
Anguis</td><td colspan="4">Well-developed</td></tr>
<tr><td colspan="2">Well-developed</td><td rowspan="2">Short</td><td rowspan="2">Narrow</td></tr>
<tr><td>Short & reduced</td><td>Absent</td></tr>
<tr><td>Xenosauridae
Shinisaurus</td><td colspan="4">Well-developed</td></tr>
<tr><td>Helodermatidae
Heloderma</td><td colspan="4">Well-developed</td></tr>
<tr><td>Varanidae
Varanus</td><td colspan="4">Well-developed</td></tr>
<tr><td>Diplometopon</td><td>Absent</td><td colspan="2">Absent</td><td>Narrow</td><td>Short</td></tr>
<tr><td>Trimeresurus</td><td colspan="4">Absent</td></tr>
</table>

The pectoral girdle is seen to be well developed in most lepidosaurs except chamaeleons, some limbless anguids, *Diplometopon* and *Trimeresurus*, where it is reduced or absent. In *Caiman*, the clavicle is absent.

CHARACTER DISTRIBUTION AND PHYLOGENY

6- Intraspecific and interspecific variation

Before we can assess the phylogenetic value of characters from the osteology and musculature of the neck region in different groups, we need to identify those characters that are too labile to be used. These include characters that vary with ontogeny, sexual dimorphism, or between individuals (Rensch, 1959; Gould, 1966). Similarly, since we are frequently comparing genera, we also need to be able to identify characters that vary between the different species of a single genus.

Note: In the descriptions, the numbers after some of the osteological and muscular characters are those of the character in the phylogenetic discussion below.

Intraspecific variation

Clearly, neither time nor availability of specimens permitted multiple dissections of all species. However, this was possible for three taxa. These were the agamid *Uromastyx aegyptia* (juvenile + adult), the gekkonid *Gekko gecko* (small + large specimen), the teiid *Kentropyx calcarata*. It was not possible to investigate sexual dimorphism.

Intraspecific osteological variation

Skull

1- Nature of the posterodorsal margin of the parietal (smooth or with concavities) [*Uromastyx aegyptia* and *Gekko gecko*].

2- The ventrolateral margin of the oto-occipital (straight or concave) [*Uromastyx aegyptia* and *Gekko gecko*].

3- The shape and size of the epiphyses of the basal tubera (oval or triangular; small or large) [*Uromastyx aegyptia* and *Gekko gecko*].

4- The size of squamosal (small or large), [*Kentropyx calcarata*].

These characters were excluded from the phylogenetic discussion.

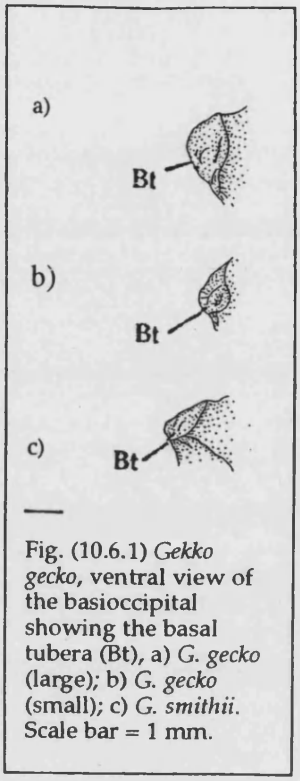


Fig. (10.6.1) *Gekko gecko*, ventral view of the basioccipital showing the basal tubera (Bt), a) *G. gecko* (large); b) *G. gecko* (small); c) *G. smithii*. Scale bar = 1 mm.

Presacral vertebral column

1- Number, size and position [66] (sutured, fused to the centrum front or behind) of the intercentra [*Uromastyx aegyptia, Gekko gecko*] (Fig., 10.6.2a-d).

2- The number and size of the basal and lateral crests (one or two, small or large) [*Gekko gecko*].

3- The shape of the dorsal tip of the neural spines (oval or triangular) [*Uromastyx aegyptia*].

Pectoral girdle:

1- Length of the lateral arms of the interclavicle (short or long) [*Uromastyx aegyptia*].

2- Clavicle perforation (present or absent) [*Kentropyx calcarata*].

Note: Some characters were observed only in a few taxa, and therefore lack character numbers. Character [66] was included in the analysis but treated with caution.

Table (10.6a) below shows the osteological variation within Teiidae (*Kentropyx calcarata* - intraspecific).

Species / Osteological characters	*K. calcarata* (dissected specimen)	*K. calcarata* (skeletal specimen)
Dorsal process of squamosal	Small	Large
Clavicle ventral side	Perforated	Solid

Table (10.6b) below shows the osteological differences within Agamidae* (adult and juvenile *Uromastyx* - intraspecific variation).

Species / Osteological characters	Juvenile	Adult
Mid-posterodorsal margin of the parietal	Smooth	Posterior process
Ventrolateral margin of the oto-occipital	Straight	Concave
Epiphyses of the basal tubera	Triangular	Oval
1st intercentrum	Pointed	Wide
Spine tips	Rounded	Triangular
No. of intercentra	4 small	5-6 large
Position of intercentra	Sutured	Fused to centrum behind
Lateral arms of the interclavicle	Short	Long

Table (10.6c) below shows osteological differences within Gekkonidae (between two individuals of *Gekko gecko* [small & large]).

Species / Osteological characters	*G. gecko* (small)	*G. gecko* (large)
Shape of mid-posterodorsal process of the parietal	Long	Short
Nature of the mid-line ridge of supraoccipital	Rounded	Keeled
Shape of posterolateral process of the parietal	Narrow	Wide
Shape of paroccipital process	Narrow	Wide
Shape of the ventrolateral margin of the oto-occipital	Expanded more laterally (convex)	Straight
Size of the epiphysis of the basal tubera	Small	Large
Size and shape of anterior keeled intercentra	Small, narrow and pointed anteriorly	Large, wide and pointed anteriorly and posteriorly
No. of lateral crests on the 3rd intercentrum	1	2
Size of the basal crests	Small	Large

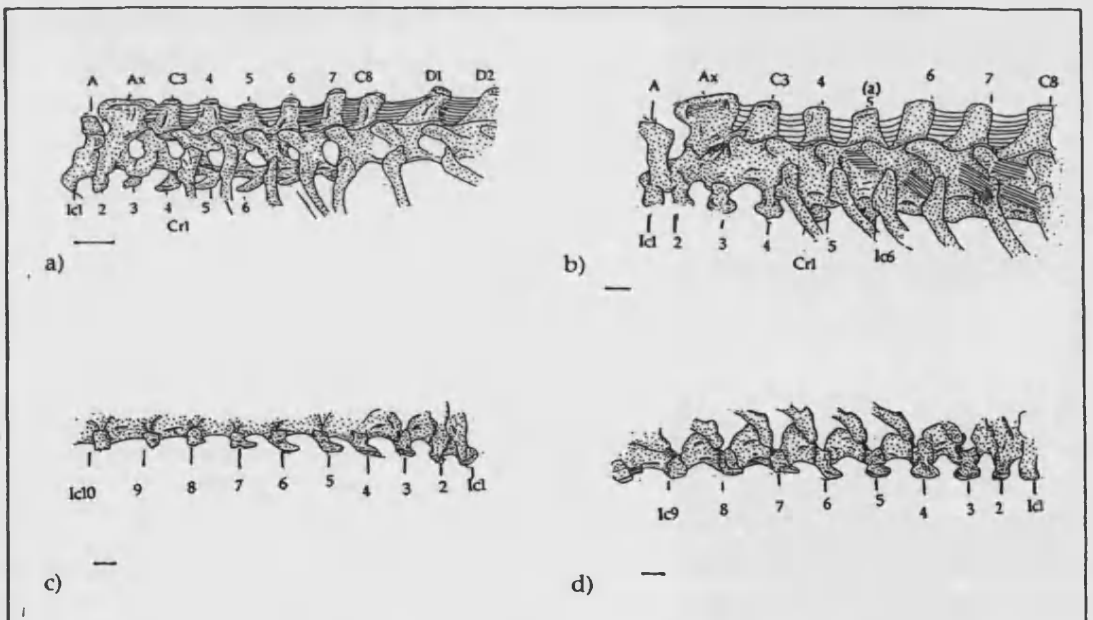


Fig. (10.6.2) *Gekko gecko*, a) small specimen, left lateral view of the cervical vertebrae. b) Large specimen, left lateral view of the cervical vertebrae (C). c) Small, right ventrolateral view of the cervical and dorsal vertebrae with 8 keeled intercentra (Ic). d) Large, right ventrolateral view of the cervical and dorsal vertebrae showing 8 keeled intercentra and 9th intercentrum with small elevation (large). Scale bar = 1 mm.

Intraspecific muscular variation

Intermediate and deep muscles (significant variation only within *Uromastyx aegyptia*):

1- Origin of clavicle dorsalis (muscle fascia and/or skull) [11]; longus colli (C8 or D1) [33] (Fig., 10.6.3a-b); longus colli tendon (C2 or C4); longus cervicus (C6 or C8).

2- Insertion of episternocleidomastoid (paroccipital and/or parietal); longissimus capitis 4 (basioccipital and/or oto-occipital); longissimus capitis minor (basioccipital and/or oto-occipital).

3- Number of deep muscle slips to suprascapula (one or two) (Fig., 10.6.3c-d); splenius capitis bundles of origin (4 or 5).

4- Manner of insertion of obliquus capitis on skull (dorsal or ventrolateral side of paroccipital process); longissimus capitis 2 on paroccipital process (lateral and/or ventral side); first intercentral muscle slip on basioccipital (converges or diverges); size of the deep first intercentral muscle slips to the oto-occipital (narrow or wide).

The table (10.6d) below shows muscular variation between juvenile and adult *Uromastyx*.

Species / Osteological characters	Juvenile	Adult
Insertion of episternocleidomastoid	Paroccipital process	Paroccipital process + parietal
Origin of clavicle dorsalis	Muscle fascia	Muscle fascia + parietal
No. of deep rib muscle slips to suprascapula	1 (2nd cervical rib muscle slip)	2 (2nd & 3rd cervical rib muscle slips)
Mode of attachment of obliquus capitis	Dorsal + ventrolateral side of the paroccipital process.	Dorsal side of paroccipital process
Origin of splenius capitis	C7-D3	C8-D3
Insertion of longissimus capitis 2 on paroccipital	Lateral	Lateral + ventral
Insertion of longissimus capitis 4	Basal tubera	Basal tubera + oto-occipital
Origin of longus colli	C7 + C8 rib ligament	C8 + D1 rib ligament
Beginning of tendinous insertion of longus colli	Along C2-3	Along C4
Origin of longus cervicus	C6	C8 rib ligament
Insertion of 1st intercentral muscle on basioccipital	Diverging (under longus colli insertion, ventrally)	Centrally toward each other (not under longus colli)

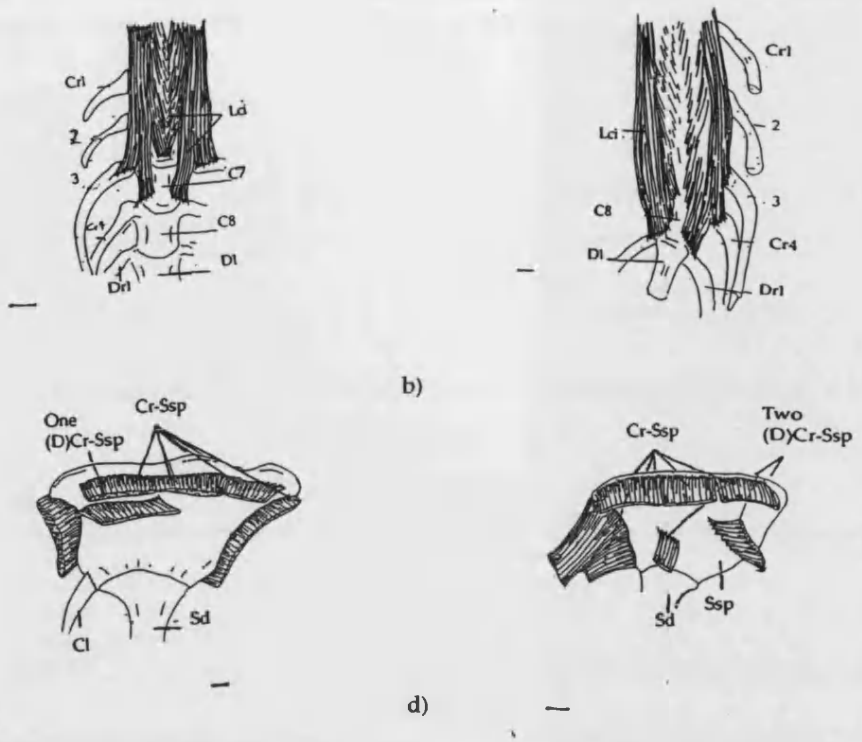


Fig. (10.6.3) *Uromastyx aegyptia* a) Juvenile, ventral view of the cervical region shows the beginning of longus colli on C7; b) Adult, ventral view of the cervical/dorsal region shows the Start origin of longus colli from D1; c) juvenile, left lateral view of the pectoral girdle showing the one deep muscle slip to suprascapula (D) Cr-Ssp; d) Adult, right lateral view of the pectoral girdle showing the two deep muscle slips to suprascapula(D) Cr-Ssp. Scale bar = 1 mm.

Interspecific variation

Exploration of interspecific variation was limited to a relatively small number of examples: *Anolis* (iguanids), *Chamaeleo* (chamaeleonids), *Hemidactylus* and *Gekko* (gekkonids), *Scincus* and *Tiliqua* (scincids), *Cordylus* (cordylids), *Lacerta* (lacertids), *Varanus* (varanids) and *Diploglossus* (anguids). Some of the variable characters are identical to those listed under intraspecific variation. Those have been excluded from the lists below.

Interspecific osteological variation

Skull

1- Shape of the superior surface of the supraoccipital (flat, rounded, keeled) [*Diploglossus*, *Tiliqua*].

2- Size, and presence or absence of supratemporal [62] [*Chamaeleo, Scincus*].

3- Shape of the area between the basal tubera of the basioccipital (smooth, ridged) [*Diploglossus*]; and basal tubera size (wide, narrow) [*Varanus*] (Fig. 10.6.4a-c).

Presacral vertebral column

1- Presence or absence of mid-central ridges [*Chamaeleo*].

2- Number of cervical ribs and rib ratio (3 – 5) [*Varanus*].

3- Shape of the cervical rib shafts (smooth or bearing posterior process) [*Anolis, Diploglossus*].

4- Shape of the posterior process of the atlas (long or short) [*Anolis, Lacerta, Varanus*].

5- Shape of the postzygapophyses of the axis (tubercles or posterior processes) [*Anolis, Chamaeleo, Lacerta*].

6- Size of the axis transverse process (long or short) [*Anolis*].

7- Separation or fusion of anterior intercentra [*Diploglossus, Anolis*].

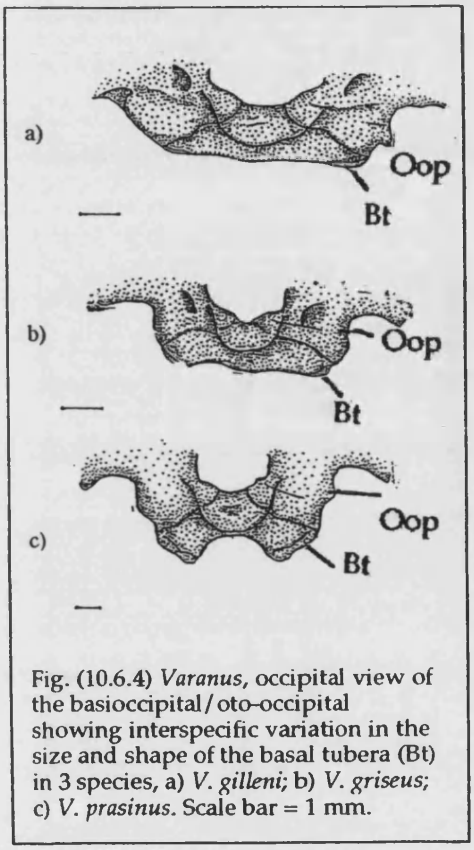
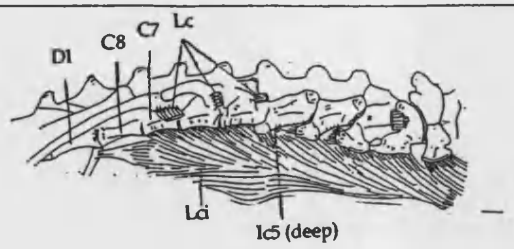


Fig. (10.6.4) *Varanus*, occipital view of the basioccipital/oto-occipital showing interspecific variation in the size and shape of the basal tubera (Bt) in 3 species, a) *V. gilleni;* b) *V. griseus;* c) *V. prasinus*. Scale bar = 1 mm.

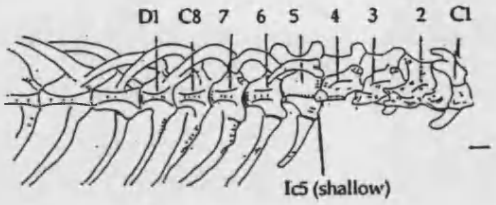
8- Size of intercentra (large, small) [*Anolis*] (Fig., 10.6.5a- b).

Pectoral girdle

1- Clavicular articulation (scapula or suprascapula or both) [*Anolis*].



a)



b)

Fig. (10.6.5) a) *Anolis richardii*, right ventrolateral view of the cervical region showing the strongly keeled 5th intercentrum (Ic5). b) *Anolis edwardii*, right ventrolateral view of the cervical region showing the small keeled 5th intercentrum (Ic5). Scale bar = 1 mm.

Table (10.6e) below shows osteological variation in Iguanidae* (among 3 species of *Anolis*).

Species / Osteological characters	*A. richardii*	*A. edwardii*	*A. biporcatus*
Mid-posterodorsal margin of parietal	Possesses posterior process	Smooth	Possesses posterior process
Ventrolateral margin of oto-occipital	Convex	Convex	Straight
Epiphyses of the basal tubera	Triangular	Triangular	Oval
Posterior process of atlas	Long	Long	Short
Postzygapophyses of axis	Tubercles	Posterior process	Smooth
Transverse process of axis	Long	Short	Short
2nd & 3rd cervical rib shafts	Smooth	Bear posterior processes	Smooth
Clavicle articulation	Suprascapula	Suprascapula	Scapulocoracoid

Table (10.6f) below shows osteological variation in Chamaeleonidae (between 4 species of *Chamaeleo*).

Species / Osteological characters	*C. chameleon*	*C. jacksonii*	*C. vulgaris*	*C. dilepis*
Supratemporal	Absent	Present	Absent	Absent
Axis postzygapophyses	Tubercles	Smooth	Smooth	Tubercles
No. of intercentra	5	2	3	4
Position of intercentra to centra	Centred	Fused behind	Fused behind	Fused behind

Table (10.6g) below shows osteological variation in Gekkonidae (between two species of *Gekko*).

Species / Osteological characters	*G. gecko*	*G. smithi*
Shape of mid-posterodorsal process of the parietal	Short	Long
Shape of squamosal	Round	Keeled
No. of lateral crests on the 3rd intercentrum	2	1
No. of intercentrum	8	7

Table (10.6h) below shows osteological variation in Gekkonidae (between 2 species of *Hemidactylus*).

Species / Osteological characters	*H. flaviviridis*	*H. fasciatus*
Size of the lateral crests of the 2nd intercentrum	Wide	Narrow
Size & shape of the posterior intercentra	Wide	Narrow

Table (10.6i) below shows osteological variation in Scincidae (between 2 species of *Scincus*).

Species / Osteological characters	*Scincus miternus*	*Scincus alifasciatus laterimaculatus*
Size of supratemporal	Long	Short
2nd intercentrum	With lateral crests	Smooth
Position of 3rd intercentrum	Fused to C2	Sutured between C2 & C3
No. of intercentra	7	6
Position of intercentra	Fused to centrum in front	Fused between centra

Table (10.6j) below shows the osteological variation in Cordylidae (between 2 species of *Cordylus*).

Species / Osteological characters	*C. polyzonus*	*C. warreni*
No. of intercentra	5	4

Table (10.6k) below shows osteological variation in Lacertidae (between 2 species of *Lacerta*).

Species / Osteological characters	*L. trilineata*	*L. lepida pater*
Postzygapophyses surface	Tubercles	Posterior processes
No. of intercentra	8	7
Neural spine tips	Compressed	Triangular

Table (10.6l) shows osteological variation in Anguidae (between 3 species of *Diploglossus*).

Species / Muscular characters	*D. crusculus*	*D. shamini*	*D. monotrofis*
Nature of midline ridge of supraoccipital	Rounded	Not-observed	Keeled
Shape of epiphyses of basal tubera	Oval	Oval	Elongated
Shape of central area between basal tubera	Smooth	Smooth	Median ridge
Development of intercentra	Deep with sharp apex	Short with rounded apex	Deep with sharp apex
Separation or fusion of anterior intercentra	Fused togather	Separated	Separated
Nature of cervical rib shafts	Smooth	Ridged	Smooth

Interspecific muscular variation

Deep muscles

1- Origin of spinalis capitis (C1-3 or C1-4) [*Varanus*].

2- Insertion of episternocleidomastoid (braincase, parietal, lateral skull components) [*Chamaeleo, Cordylus*] (Fig., 10.6.6a).

3- Area of initial origin of longus colli (anterior or posterior edge of centrum) [*Chamaeleo, Tiliqua, Scincus*] (Fig., 10.6.6b).

4- Number of intercentral muscle slips to skull [49] (2-5) [*Chamaeleo, Varanus*], and area of insertion [56] (basioccipital or basioccipital and oto-occipital)[*Varanus*] (Fig., 10.6.6c).

5- Mode of origin of depressor mandibulae externus (dorsally or laterally) [*Varanus*].

6- Shape of insertion of longus colli (curved or straight) [*Varanus*]; and longus colli tendon [*Cordylus*] (Fig., 10.6.6d).

Table (10.6m) below shows muscular variation in Chamaeleonidae (between 4 species of *Chamaeleo*).

Species / Muscular characters	*C. chamaeleo*	*C. jacksonii*	*C. vulgaris*	*C. dilepis*
Dorsal rib muscle slips to suprascapula	Present	Absent	Absent	Present
Insertion of longissimus capitis 2	Paroccipital + supratemporal + squamosal	Squamosal	Paroccipital + supratemporal + squamosal	Paroccipital + supratemporal + squamosal
Initial point of origin of longus colli (vertebral level)	D3	D2	D3	D2
Initial point of origin of longus colli (position on bone)	Posterior edge	Posterior edge	Posterior edge	Anterior edge
No. of intercentral muscle slips to skull	5	2	3	4

Table (10.6n) below shows muscular variation in Scincidae (between 2 species of *Scincus*).

Species / Muscular characters	*Scincus miternus*	*Scincus alifaciatus laterimaculatus*
Insertion of episternocleidomastoid	Quadrate, squamosal, supratemporal and parietal	Quadrate, squamosal and parietal
Origin of longus colli	D2 & D3 rib ligament	D1 & D2 rib ligament

Table (10.6o) below shows muscular variation in Scincidae (between 2 species of *Tiliqua*).

Species / Muscular characters	*Tiliqua rugosa*	*Tiliqua nigrolutea*
Origin of splenius capitis	C4-8	C7-D2
Origin of longus colli	C8-D1 rib ligament	D2 centrum
Tendon of insertion of longus colli	Long	Short

Table (10.6p) below shows muscular variation in Cordylidae (between 2 species of *Cordylus*).

Species / Muscular characters	*C. polyzonus*	*C. warreni*
No. of rib to suprascapula muscle slips	3	4
Origin of splenius capitis	C7-D1	C8-D2
Insertion of longissimus capitis 2	Parietal + supratemporal + paroccipital process	Parietal + paroccipital process
Tendon of insertion of longus colli starts below	C5	C4

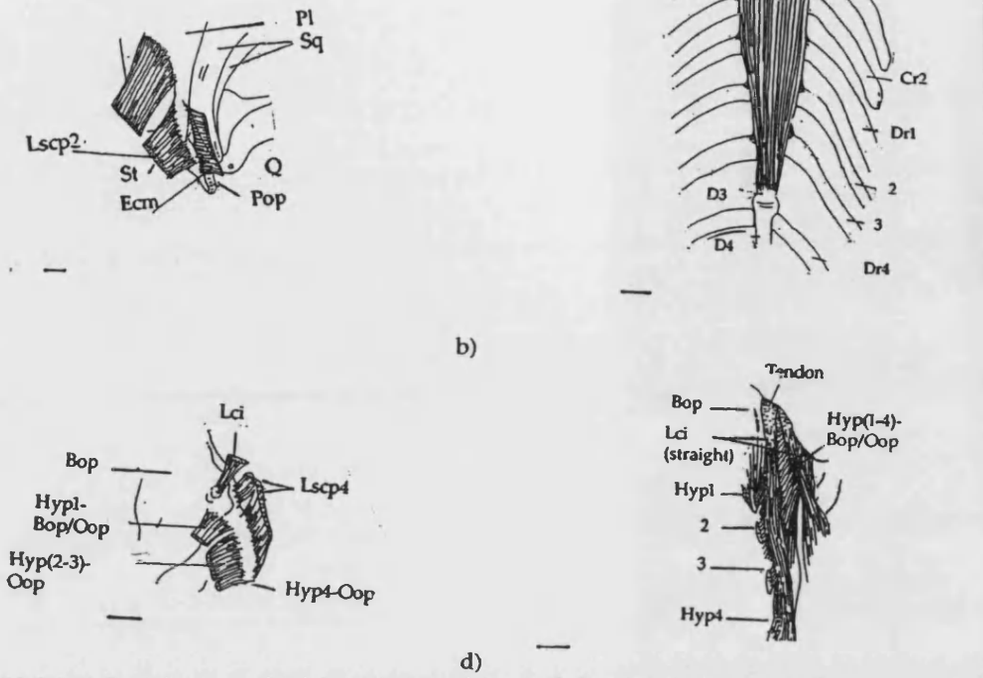


Fig. (10.6.6) a) *Cordylus warreni*, left lateral view of the skull showing the insertion of episternocleidomastoid (Ecm) on paroccipital process, supratemporal and parietal, while in *C. polyzonus*, the episternocleidomastoid (Ecm) inserts on the parietal (Pl) and lateral skull components. b) *Chamaeleo vulgaris*, ventral view of craniocervical region showing the longus colli (Lci) beginning from D3 unlike other dissected *Chamaeleo* species where longus colli (Lci) begins from D2 or D4. c) *Varanus jobiensis*, ventral view of the basioccipital (Bop) showing the insertion of the first hypapophysis (Hyp1-Bop/Oop) muscles on the basioccipital and oto-occipital rather than basioccipital only (*V. griseus*). d) *Varanus jobiensis*, ventral view of the craniocervical region showing the straight insertion of longus colli (Lci), while in *V. griseus* it inserts as a curved tendon. Scale bar = 1 mm.

Summary

The relatively high level of intraspecific and interspecific variation for these characters means that they can only be used with care in phylogenetic discussion. Most of the features that show intraspecific or interspecific variation were not used in the phylogenetic discussion:

- Shape of the mid-dorsal margin of the parietal.
- Shape of the ventrolateral margin of the oto-occipital.
- Shape of the basal tubera.

- Presence or absence of the supratemporal.
- Shape of neural spine tips.
- Number, position and shape of intercentra.
- Presence or absence of intercentral lateral crests.
- Surface morphology of the postzygapophyses.
- Size of the posterior process of the atlas and the transverse process of the axis.
- Number and shape of the cervical ribs.
- Presence or absence of ventral perforation of clavicle.
- Area of articulation of clavicle on suprascapula or scapulocoracoid.
- Size of the lateral arm of the interclavicle.

However, the distribution of a few other characters were explored with caution:-

1- Intraspecific variation

Osteology = [66] (show intra/and interspecific variation 0-1 state) = position of intercentra in relation to centra.
Myology = [11] (show intraspecific variation 0-1 state) = origin of clavicle dorsalis.
[55] (show intraspecific variation 0-1 state)= insertion of longissimus capitis 4

2- Interspecific variation

Osteology = [62], [67] (both show interspecific variation 0-1 state & 4-5 state) = presence or absence of supratemporal and articulation of first cervical rib.

Myology = [12] (show interspecific variation 0-1 state) = origin of rib muscle slips to suprascapula and scapulacoracoid.
[19] (show interspecific variation 0-1 state) = splenius capitis extension.
[33] (show interspecific variation 0-1 state) = origin of longus colli.
[49] (show interspecific variation 1-3 state) = number of postatlantal intercentrum to skull muscle slips.

The intra/ and interspecific variation found in characters like [66], [62], [12] and [19] are not consistent within states, therefore they should be used with care in the phylogenetic discussion, or removed.

Characters like [11], [55], [67], [33] and [49] show intra/ and interspecific variation within and between species, but the character state could be changed to encompass the variation within the states (e.g. states of character [11] could be change to (0) skull roof; (1) muscle fascia +/- skull roof; (2) muscle absent).

In characters like [45] and [27] the variation is consistent within the state.

7- Character distribution and discussion

Cladistics has become the most widely used methodology for phylogenetic analysis (Forey et al., 1992). Such analysis evaluates character states to determine whether they might be primitive (plesiomorphic) or derived (apomorphic), and then looks for patterns of shared derived characters (synapomorphies) that support hypotheses of common ancestory (monophyly, Hennig, 1966).

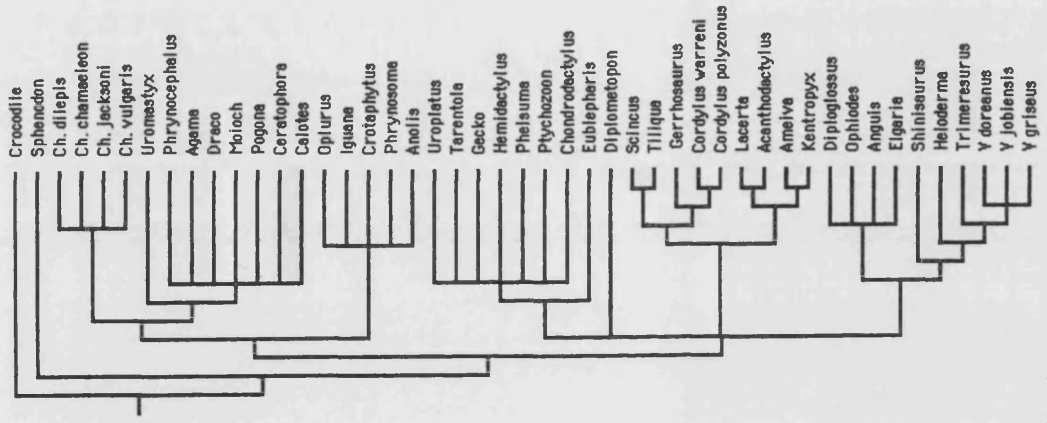


Fig. (10.7) a consensus tree based on the work of Estes et al. (1988) and Gauthier et al. (1988) which I used to plot the distribution of my craniocervical characters.

A selection of craniocervical characters of Squamata, *Sphenodon* and *Caiman* will ultimately be included into a larger matrix of characters. However, since there are currently many debates on squamate systematics and character significance, I did not attempt to construct a new tree. Instead I examined the distribution of my craniocervical characters using a consensus tree based on the work of others (e.g. Estes et al., 1988; Gauthier et al., 1988 - see Methods and Material, chapter 2), and the computer programme MacClade (Maddison and Maddison, 1992). 10 osteological and 57 muscular characters from the neck region were entered into a data matrix (Appendix).

Muscular characters

1) Origin of depressor mandibulae internus

(0) From skull roof (parietal, squamosal, supratemporal)
(*Sphenodon*, *Scincus*, Gekkota, iguanids)
(1) From skull roof + quadrate +/- paroccipital epiphyses
(*Caiman*, agamids, *Tiliqua*, cordylids, chamaeleons, lacertids, teiids, anguids, xenosaurids) or + paroccipital epiphyses – eublepharids)
(2) From quadrate only
(varanids, *Uroplatus*)
(3) From exoccipital
(*Diplometopon*)
(4) From muscle fascia
(*Trimeresurus*)

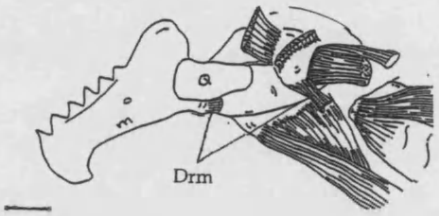


Fig. (10.7.1) *Diplometopon zarudnyi*, left lateral view of the skull showing the origin of depressor mandibulae (Drm) as one bundle from the exoccipital. Scale bar = 1 mm.

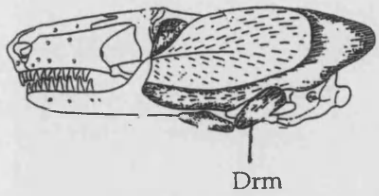
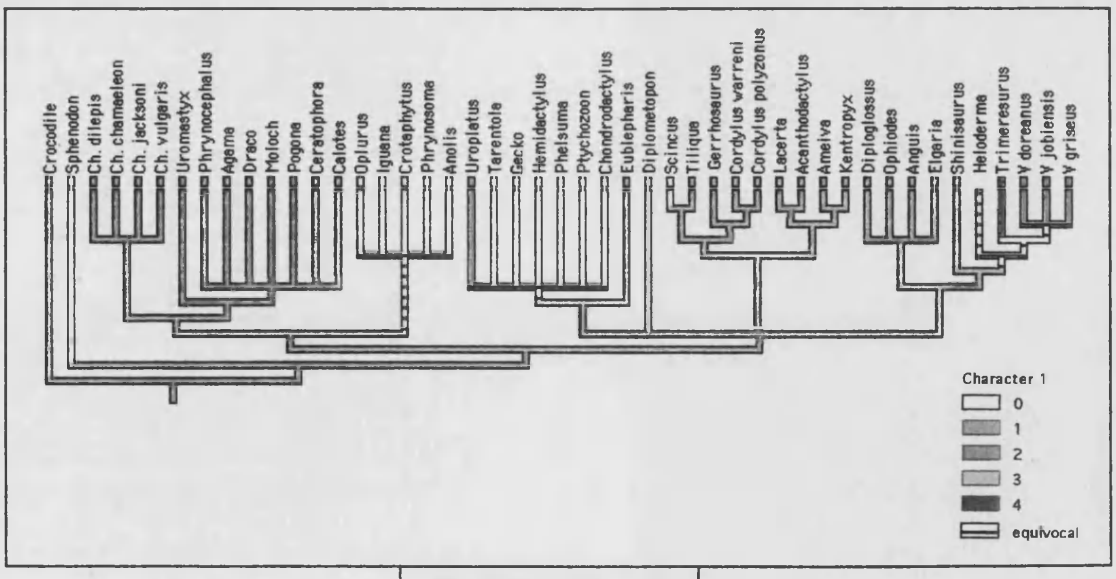
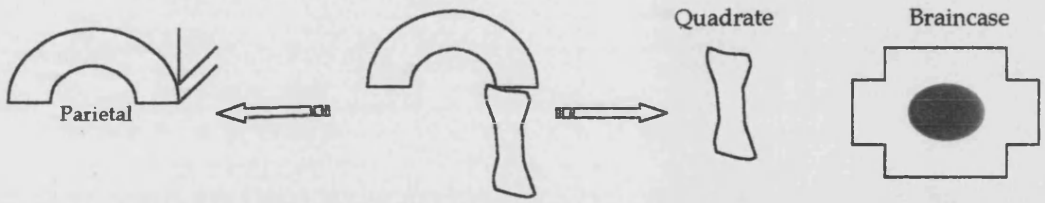


Fig. (10.7.2) *Dibamus*, left lateral view of the skull showing the origin of depressor mandibulae (dm) from braincase (Rieppel, 1984).



CHARACTER .1.

Character (1) appears primitive (plesiomorphic) because it is most widely distributed. Character (0) occurs in *Sphenodon*, at the base of iguanids, and in gekkonids (except *Uroplatus*). Character (1) seems to be plesiomorphic as it occurs in most squamates except iguanids and most Gekkonidae. Character (2) occurs as an advanced character of varanids and independently in the divergent gekkotan *Uroplatus*. Character states (3) and (4) are distinctive for the limbless *Diplometopon* and *Trimeresurus*, but only one specimen for each genus was dissected. Rieppel (1984), reported that *Dibamus* resembles amphisbaenians in the short extension of the depressor mandibulae (originates from the braincase and not the dorsal side of the skull, also in other fossorial limbless as in lizards e.g. pygopodids) (Fig., 10.7.1a-b). Clearly further dissection is needed of amphisbaenians, dibamids and a wider range of snakes to understand the distribution of this character. The shortened depressor mandibulae, which originates from the exoccipital in *Diplometopon*, may be an adaptation of the feeding mechanism to a narrower jaw opening as a result of the burrowing life style.



(0) = skull roof +/- lateral skull components, (1) = skull roof +/- lateral skull components + quadrate +/- paroccipital epiphyses, (2) = quadrate only, (3) = braincase (exoccipital or paroccipital epiphyses), (4) = Muscle fascia.

2) Origin of depressor mandibulae externus

(0) Parietal only
(*Caiman, Sphenodon,* most iguanids [except *Phrynosoma* and *Anolis*]
(1) Skull roof (parietal, squamosal, supratemporal) +/- muscle fascia
(*Anolis, Phrynosoma,* agamids, *Gecko, Chondrodactylus,* scincids, cordylids, anguimorphs)
(2) From lateral skull, quadrate +/- muscle fascia
(*Uroplatus,* chamaeleons)
(3) From only muscle fascia
(most gekkotans, lacertids, teiids, *Trimeresurus*)

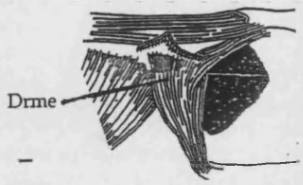
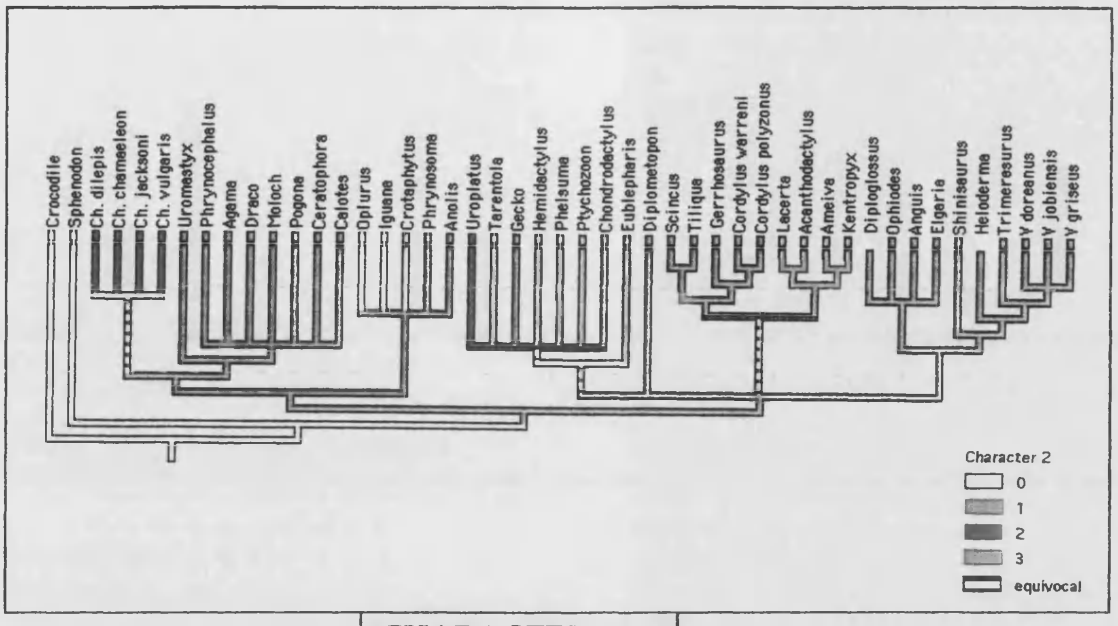


Fig. (10.7.3) *Gekko gecko,* right lateral view of the craniocervical region showing the origin of depressor mandibulae externus from muscle fascia & parietal. Scale bar = 1 mm.

The character seems to have evolved towards the loss of the attachment to the skull (0) and a shift to the muscle fascia (3). State (1) is most widespread in squamates, and could be primitive to the group with a loss of lateral attachments (squamosal and supratemporal) (Fig., 10.7.3) in some iguanians (most iguanids), or it may have arisen independently in some iguanians (base of Acrodonta) and then again at the base of Scleroglossa. Limitation of the origin to muscle fascia may have arisen independently at the base of lacertids and teiids, and at the base of gekkotans. Camp (1923), Saint Girons (1970), Estes (1983), Estes et al. (1988) and Rieppel (1988) have all supported a relationship between lacertids and teiids (lacertoids).

So character (0) is generally primitive and may have been the basal lepidosaurian condition, with expansion of origin (1) at the base of Squamata (with a reduction [2] in chamaeleons and a further reduction [3] in lacertoids and some other taxa).



CHARACTER .2.

3) Origin of cervicomandibularis

(0) From muscle fascia of splenius capitis
(most groups)
(1) From parietal and muscle fascia
(*Diplometopon*)
(2) Cervicomandibularis either absent or
from the enlarged squamosal
(chamaeleons)

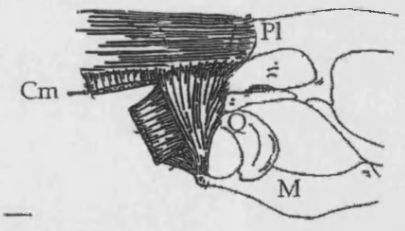
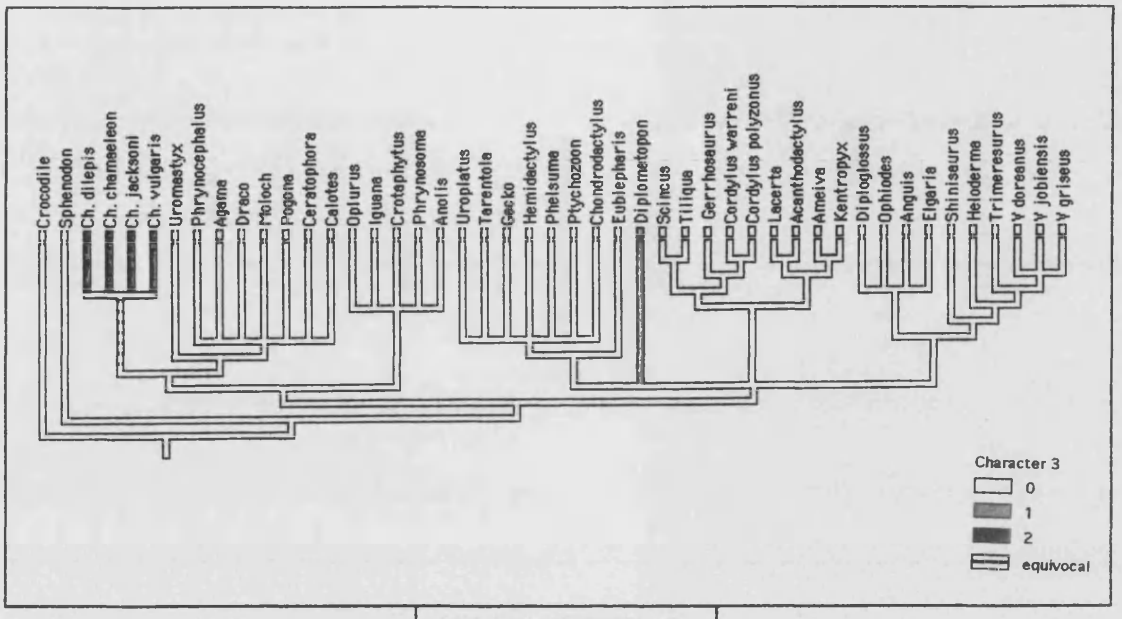


Fig. (10.7.4) *Ameiva ameiva*, right lateral view of the craniocervical region showing the origin of cervicomandibularis (Cm) from muscle fascia of splenius capitis. Scale bar = 1 mm.

Character state (0) is most widespread (plesiomorphic) (Fig., 10.7.4), while state (1) is a derived character found only in *Diplometopon* (further dissection is needed including dibamids). Within iguanians, character state (2) may be an

apomorphy of chamaeleons but further dissection is needed of other chamaeleon genera. In *Diplometopon*, the extra head of the muscle may assist in jaw opening since the inner depressor internus is reduced (see character 1).

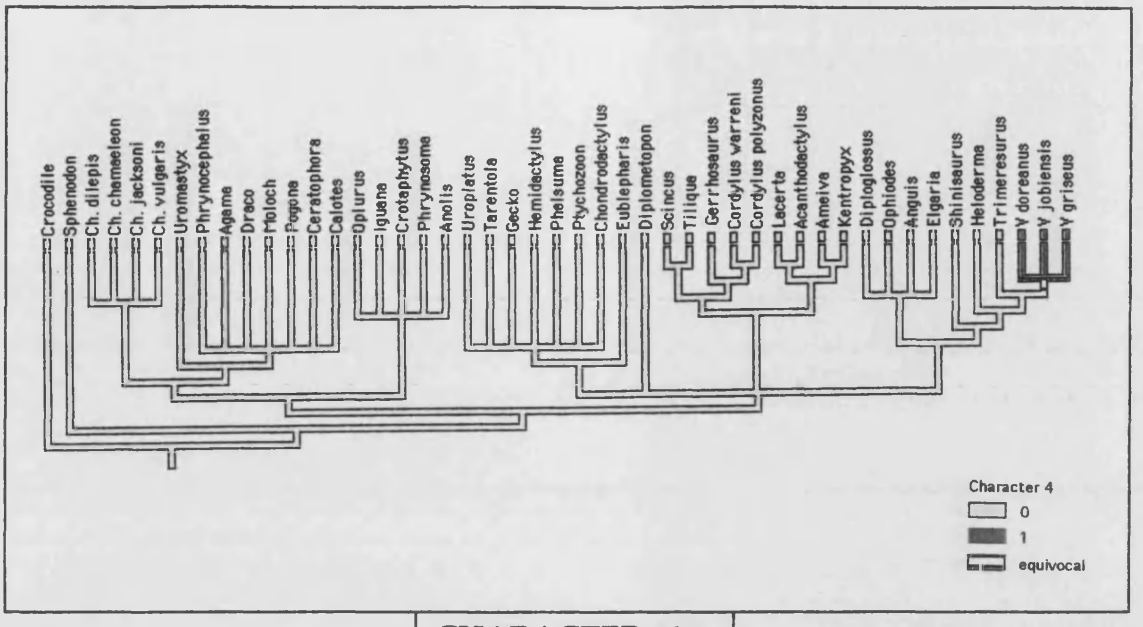


CHARACTER .3.

4) Insertion of constrictor colli

(0) On fascia of longissimus dorsi + capitis
(most groups)
(1) On muscle fascia and paroccipital process
(varanids)

Character state (0) is considered plesiomorphic. State (1) appears to be a synapomorphy of varanids. A dissection of *Lanthanotus* would be interesting. This strengthened attachment may assist in supporting the connection between the long neck (C9) and the skull, or it may be important in swallowing large prey. Constrictor colli apparently aids in the movement of prey down the pharynx (Schwenk, 2000).

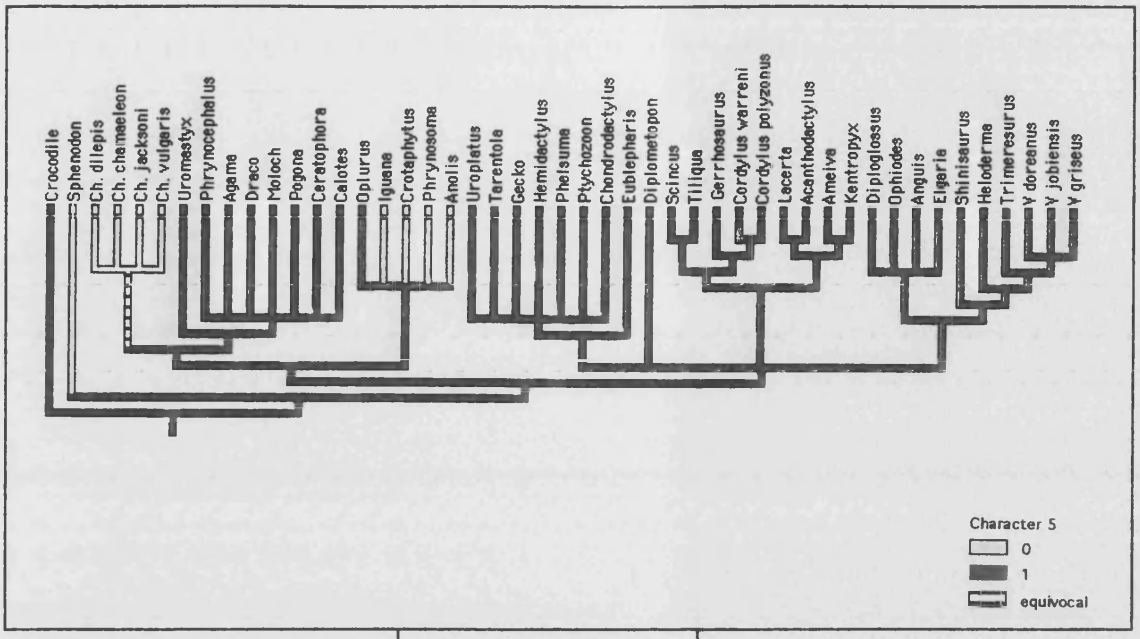


CHARACTER .4.

5) Origin of trapezius

(0) Muscle fascia of splenius capitis and longissimus dorsi
(*Sphenodon*, chamaeleons, iguanids [except *Oplurus*])
(1) Mid-dorsal line (neural spines)
(all other groups)

Character state (1) is widely distributed and is probably primitive in man and other mammals, where the muscle also originates from the spines in the mid-dorsal line (Clemente, 1985), and extends along the posterior edge of the parietal (Filan, 1990) as well as the pectoral girdle. State (0) occurs in *Sphenodon*, in chamaeleons and in a subset of iguanids, but it would be interesting to dissect more chamaeleons and iguanids. It is possible that state (0) occurred at the base of Iguania, with reversal in agamids and *Oplurus*, but this is less parsimonious. The difference in *Oplurus* might be explained by its long geographical isolation from most other "iguanids" on Madagascar. Unfortunately, its Madagascar sister taxon *Chalarodon* (Etheridge and de Queiroz, 1988) was not available for study.



CHARACTER .5.

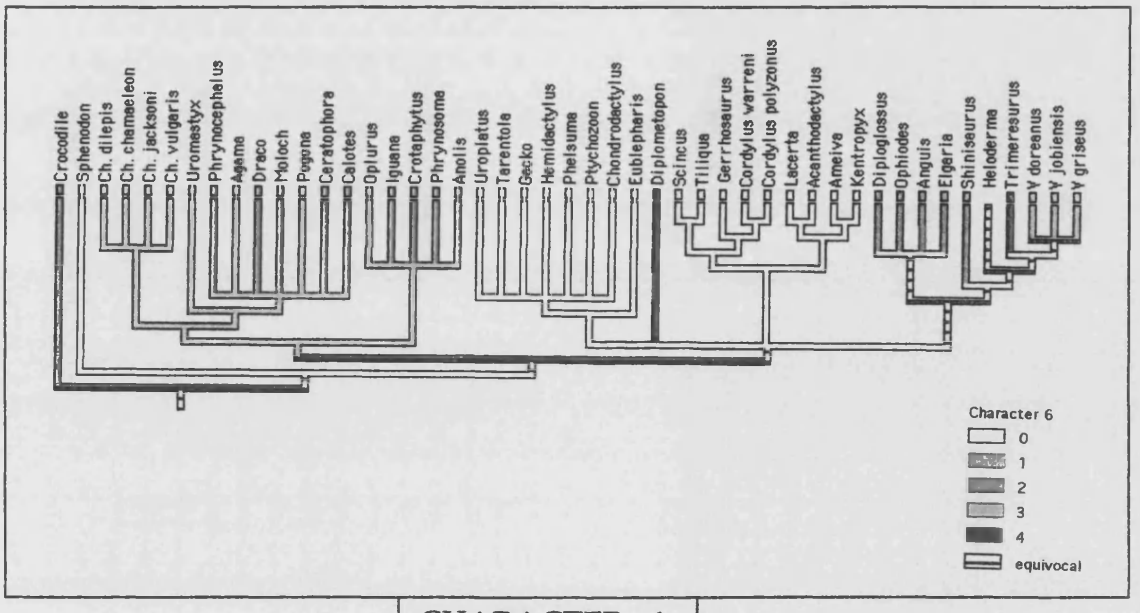
6) Insertion of trapezius

(0) Clavicle +/- scapulocoracoid or suprascapula
(*Sphenodon* [clavicle], *Anolis* [clavicle + scapulocoracoid]. Gekkota and Scincomorpha [suprascapula + clavicle].
(1) Loss of clavicular attachment (so scapulocoracoid alone)
(*Caiman* [clavicle lost], *Shinisaurus*, anguids).
(2) Attachment extends to suprascapula (so scapula + suprascapula)
(Most iguanids dissected, *Moloch, Calotes, Phrynocephalus, Ceratophora, Draco* (also attaches to clavicle)
(3) Suprascapula only
(All other agamids dissected, *Oplurus*, chamaeleons, *Varanus*)
(4) Lost
(*Trimeresurus, Diplometopon*).

Character state (0) is widespread and probably plesiomorphic. Herrel and De Vree (1999) recorded the attachment of the trapezius muscle to the clavicle in helodermatids (as in *Sphenodon*), and Clemente (1985) reports the same attachment in man. In all gekkotans and scincomorphs the muscle inserts only on the clavicle and suprascapula. State (1) is a synapomorphy of most anguimorphs with reversal in varanids (3). Extension to the suprascapula

appears to be a synapomorphy of iguanians (2), with subsequent restriction to the suprascapula (3) in many agamids although *Draco* is unusual because the muscle inserts on the suprascapula, scapulocoracoid and widely on the clavicle. Perhaps this is a secondary expansion of the attachment providing additional shock-absorption for the forelimbs when landing from a glide (Evans, 1982).

NB: State (0) occurs in man (Clemente, 1985) and in mammals generally. The muscle was not investigated during dissection in *Heloderma*.



CHARACTER .6.

In limbless amphisbaenians and snakes the muscle is lost with the clavicle and most of the pectoral girdle, but it would be interesting to dissect the amphisbaenian *Bipes* (with well-developed pectoral girdle).

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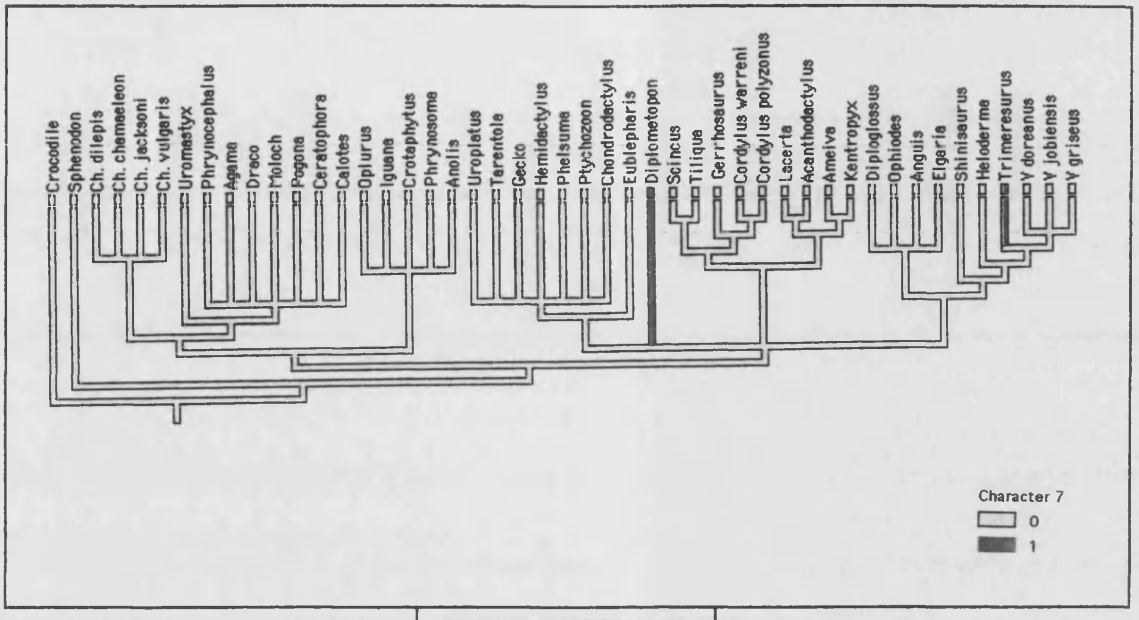
7) Presence or absence of latissimus dorsi

(0) Present
(Most taxa)
(1) Absent
(*Trimeresurus, Diplometopon*)

Character (0) appears plesiomorphic, while state (1) occurs in snakes and amphisbaenians due to loss or reduction of the pectoral girdle.



CHARACTER .7.

8) Presence of subiliocostalis

(0) Present
(*Sphenodon, Caiman*)
(1) Absent
(squamates)

(This character is associated with loss of the dermal gastralia in squamates)

Character state (0) is plesiomorphic (presence of gastralia). In tuatara, the subiliocostalis muscle slips attach to both the hook-like uncinate processes on the posterior margin of the ribs, and trunk muscles

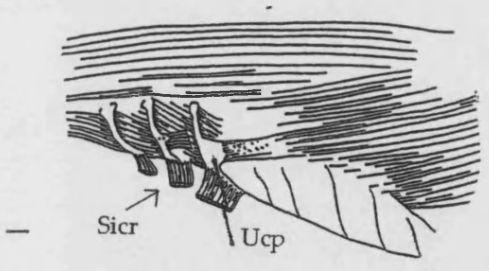
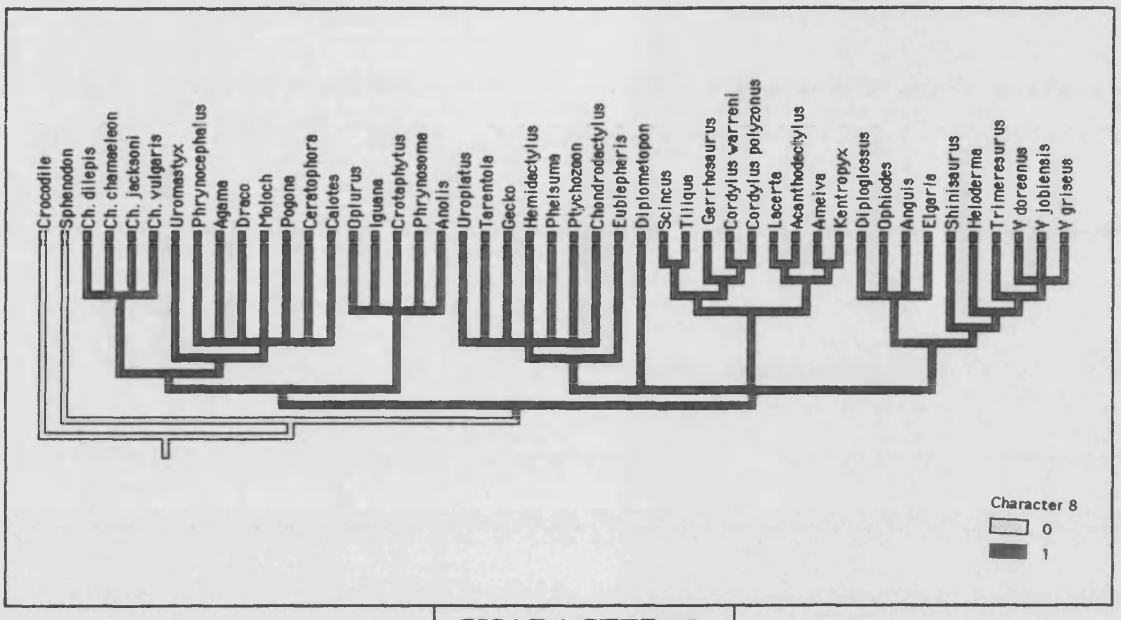


Fig. (10.7.5) *Sphenodon*, left lateral view of the cervical ribs showing subiliocostalis muscle slips (Sicr) attaching to uncinate processes (Ucp). Scale bar = 1 mm.

(Bellairs, 1969). They are directly related to the presence of gastralia, bony dermal elements protecting the ventral surface of the abdomen Gastralia were lost in the ancestry of the squamates (Carroll, 1988; Gauthier et al., 1988) and, with them, the subiliocostalis muscle (Fig., 10.7.5).



CHARACTER .8.

A similar structure occurs in crocodilians and birds (Bellairs, 1969), which retained slender gastralia beside the sternal area (Carroll, 1988).

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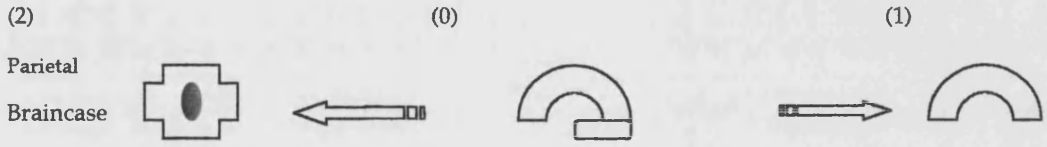
9) Insertion of episternocleidomastoid

(0) Paroccipital process +/- dorsal skull roof.
(*Sphenodon*, most iguanids, *Uromastyx*)
(1) As above but loses paroccipital attachment.
(Scincomorpha – wide insertion on skull shelf)
(2) Braincase only
(chamaeleons, most agamids, *Anolis*, gekkotans, anguimorphs, *Diplometopon*)
(3) Absent
(*Trimeresurus*)
(4) Atlas first cervical rib
(*Caiman*)

Character state (0) probably represents the basal state of Squamata. Character state (1) is restricted to scincomorphs (parietal + lateral skull components), the monophyly of which was supported by McDowell and Bogert (1954); Savage (1963); Saint Girons (1970); Rieppel (1976); Estes (1983); Arnold (1984); Estes et al. (1988), but see Lee (1998). The insertion of the episternocleidomastoid shows intraspecific variation (e.g. *Uromastyx aegyptia* juveniles the muscle inserts on the paroccipital process, while in adults it inserts on the paroccipital process and parietal), and interspecific variation (e.g. in *Scincus miternus* the muscle inserts on the quadrate, squamosal, supratemporal and parietal, while in *Scincus alifasciatus laterimaculatus* the muscle inserts on the quadrate, squamosal and parietal). Character state (2) may have arisen independently in Acrodonta (except *Uromastyx*), anguimorphs and gekkotans (Fig., 10.7.6). Although the possession of an atlantal rib is primitive in *Caiman*, the attachment of the episternocleidomastoid is probably not, since it attaches to the mastoid region (= paroccipital) in mammals.



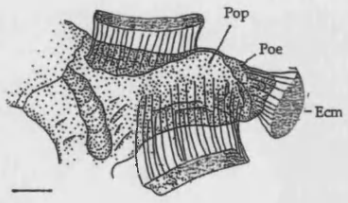
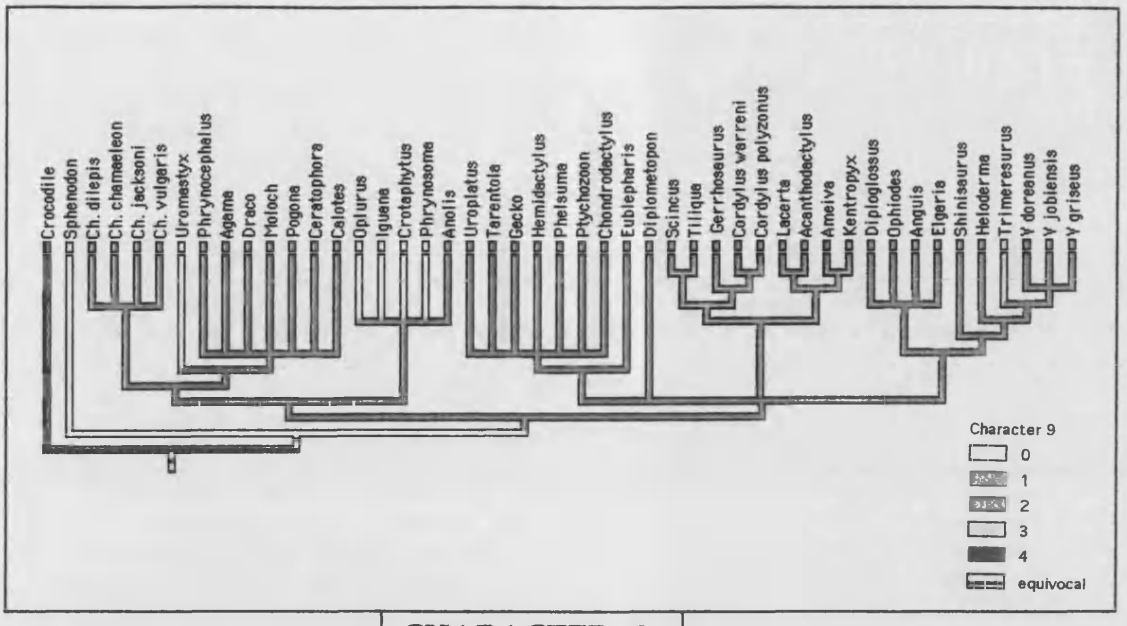


Fig. (10.7.6) *Gehyra marginata*, occipital view of the skull showing the insertion of episternocleidomastoid (Ecm) on the braincase (paroccipital epiphyses [Poe]). Scale bar = 1 mm.



CHARACTER .9.

10) Origin of episternocleidomastoid

(0) Clavicle + interclavicle
(*Sphenodon, Eublepharis*)
(1) Loss of clavicular head
(gekkonids, *Scincus, Gerrhosaurus, Shinisaurus, Elgaria,*
agamids, *Oplurus, Iguana, Crotaphytus*)
(2) Loss of interclavicular head
(varanids, *Ophiodes, Anguis*)
(3) Extra sternal head
(*Tiliqua, Cordylus,* lacertids, teiids, *Anolis, Phrynosoma, Pogona*)
(4) Sternal head only
(*Caiman, Diplometopon,* chamaeleons)
(5) Absent
(Trimeresurus)

Note: the muscle was not investigated in
Diploglossus.

Character state (0) is probably but not certainly primitive. Oelrich (1956) reported the origin of the episternocleidomastoid from the clavicle and interclavicle in the iguanids (*Ctenosaura pectinata*) as in *Sphenodon* and *Eublepharis*. Alternatively state (1) may be primitive, with an additional clavicular head gained in *Sphenodon* and eublepharids. State (2) is a

synapomorphy of varanoids, but also occurs in *Ophiodes* (Fig., 10.7.7c) and *Anguis* probably in relation to limb loss. The muscle was not investigated during dissection of *Heloderma*, but Herrel and De Vree (1999) recorded the origin of the muscle from the clavicle in this genus (2). State (3) is a synapomorphy of scincomorphs with reversal in *Scincus* and *Gerrhosaurus* (Fig., 10.7.7b). State (4) is a synapomorphy of chamaeleons but is also present in amphisbaenians (more dissection is needed). In mammals – there is a clavicular head and a sternal head (as in state 3). In birds, Berge and Zweers (1993) described no muscle by this name.

Note: when the pectoral girdle is weak the muscle originates from the sternum.

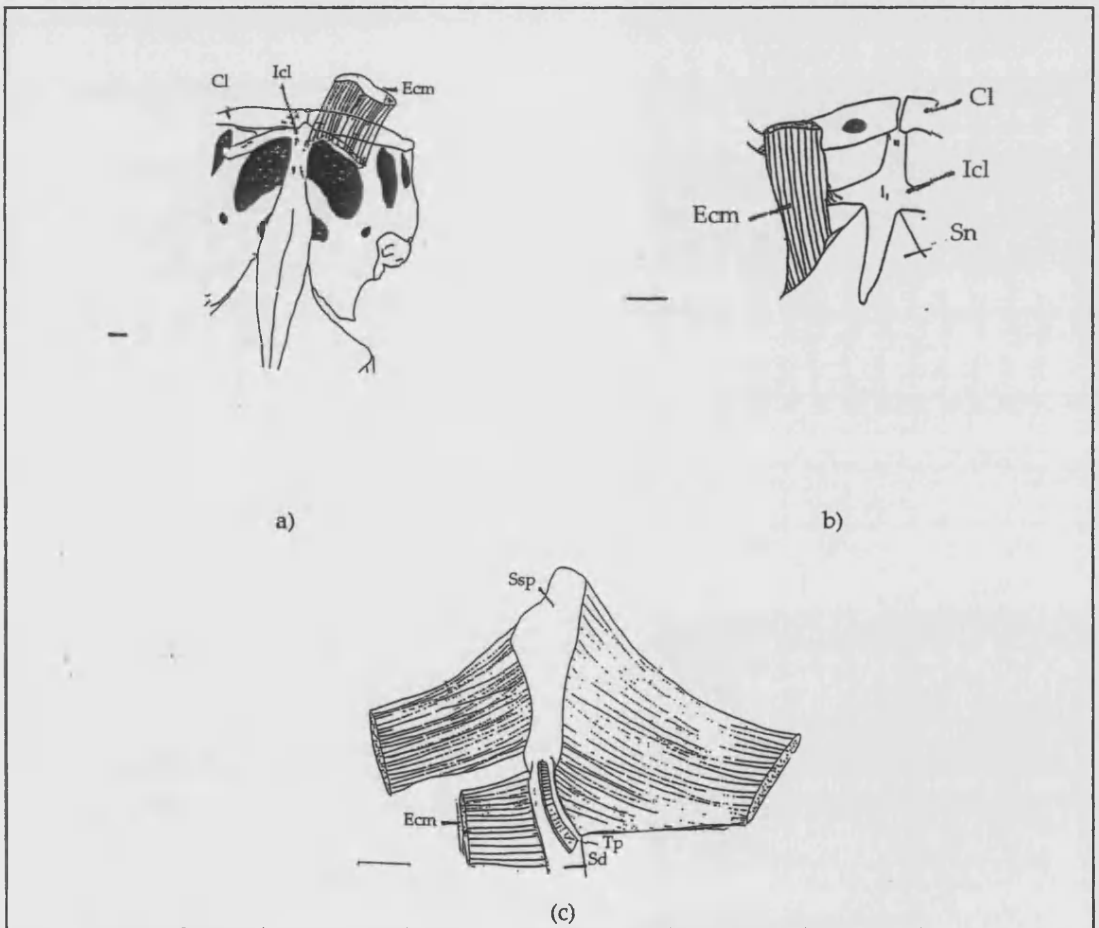
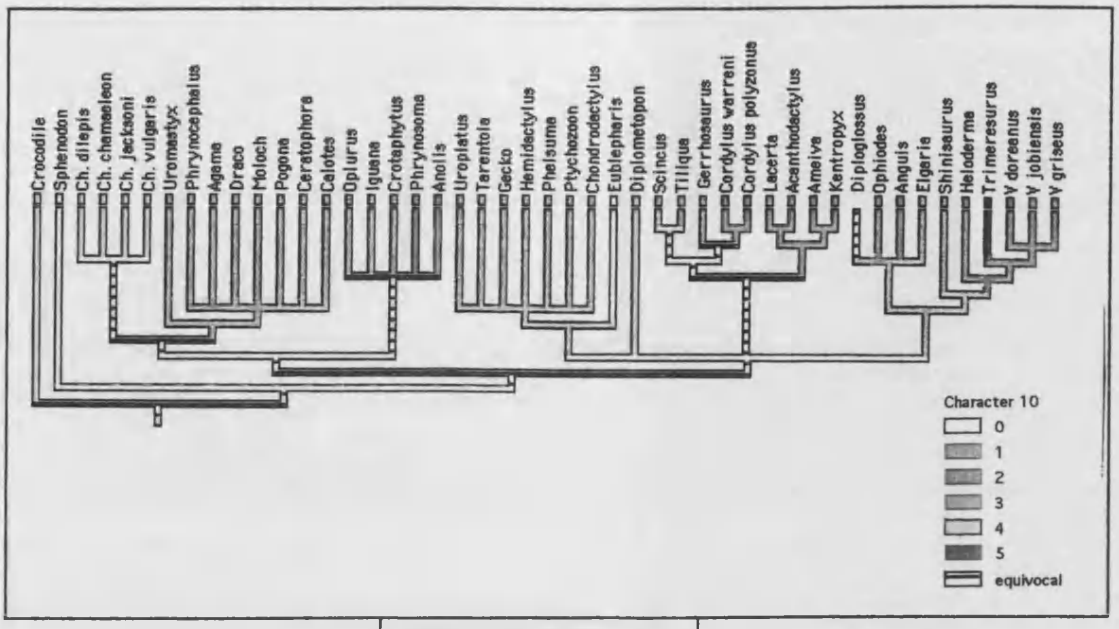


Fig. (10.7.7) a) *Iguana iguana*, ventral view of the pectoral girdle showing the origin of episternocleidomastoid (Ecm) from interclavicle (Icl). b) *Tiliqua nigrolutea*, ventral view of the pectoral girdle showing the origin of the episternocleidomastoid (Ecm) from interclavicle (Icl) & sternum (Sn). c) *Ophiodes intermedius*, left lateral view of the pectoral girdle showing the origin of episternocleidomastoid (Ecm) from clavicle (Cl). Tp = trapezius muscle. Scale bar = 1 mm.



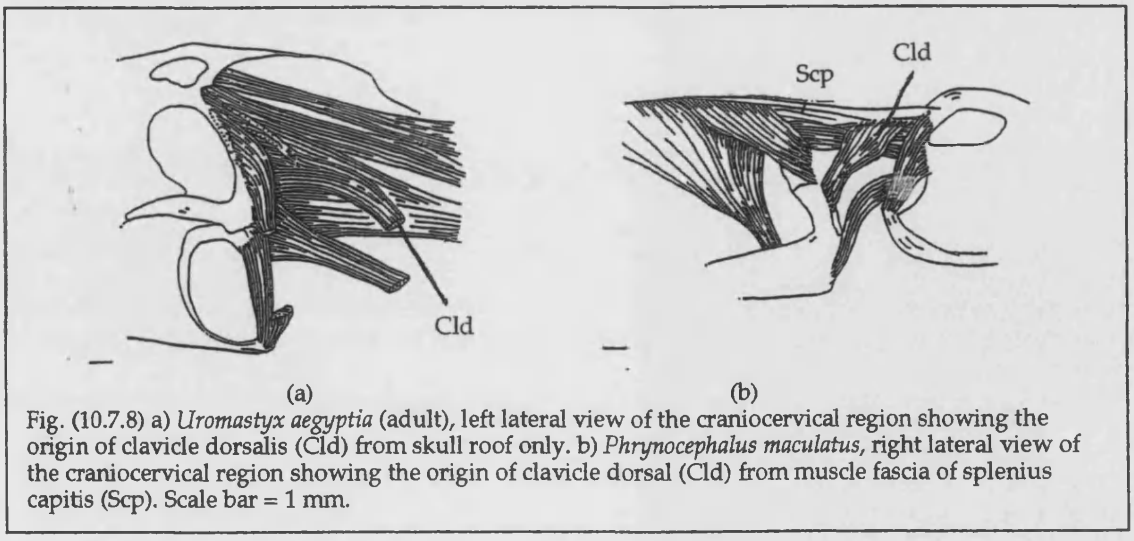
CHARACTER .10.

11) Origin of clavicle dorsalis

(0) Skull roof (parietal, supratemporal, squamosal) +/- muscle fascia
(*Sphenodon, Anolis, Iguana, Uromastyx* (adult), *Kentropyx* [parietal + muscle fascia], *Hemidactylus* [supratemporal + muscle fascia], *Phrynosoma* [squamosal only].

(1) Muscle fascia
(gekkotans [except *Hemidactylus*], scincids, cordylids, lacertids, teiids [except *Kentropyx*], *Phrynocephalus, Calotes, Uromastyx* [juvenile], *Oplurus, Ophiodes*).

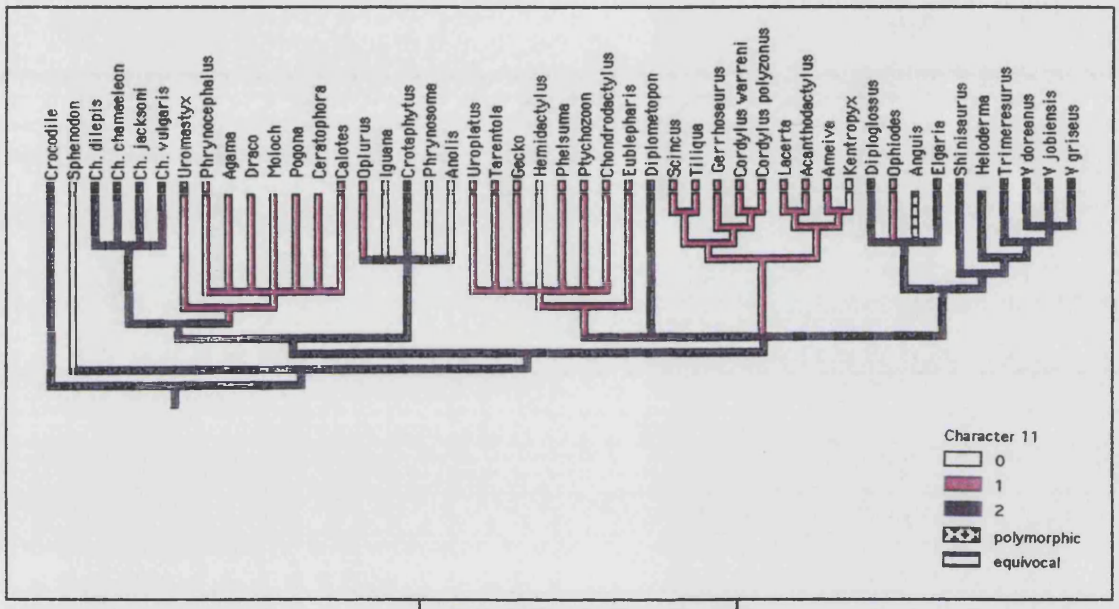
(2) Muscle absent
(*Caiman, Trimeresurus, Diplometopon,* chamaeleons [no clavicles]; anguimorphs [except *Ophiodes*], *Crotaphytus*)



(a) (b)

Fig. (10.7.8) a) *Uromastyx aegyptia* (adult), left lateral view of the craniocervical region showing the origin of clavicle dorsalis (Cld) from skull roof only. b) *Phrynocephalus maculatus*, right lateral view of the craniocervical region showing the origin of clavicle dorsal (Cld) from muscle fascia of splenius capitis (Scp). Scale bar = 1 mm.

Character state (0) may be plesiomorphic (Fig., 10.7.8a). Character state (1) is either a synapomorphy of Squamata, with reversal in some iguanids, or a synapomorphy of Scleroglossa (basal condition), or was derived independently in agamids (Fig., 10.7.8b), gekkotans and scincomorphs. State (2) is shared by most anguimorphs + snakes and amphisbaenians due to limb loss, but more dissection is needed (e.g. *Bipes*); it may be the basal squamate condition.



CHARACTER .11.

It should be noted, however, that the character shows intraspecific variation in *Uromastyx* (adult and juvenile) with respect to states (0) and (1).

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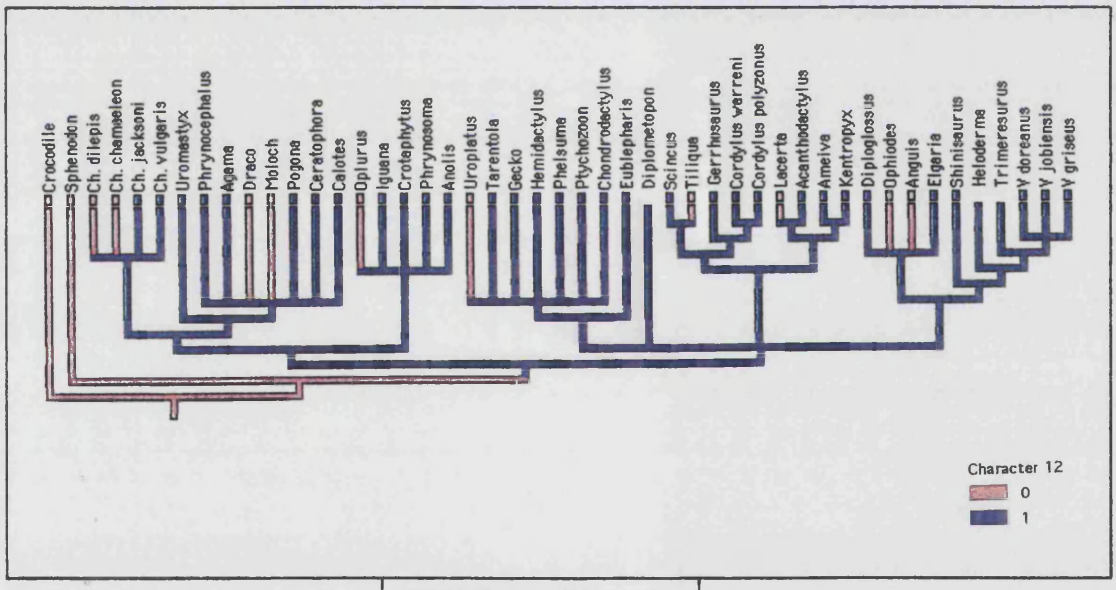
12) Origin of rib muscle slips to the suprascapula and scapulocoracoid

(0) From cervical and dorsal ribs
(*Caiman, Sphenodon, Oplurus, Moloch, Draco, C. chamaeleon, C. dilepis, Uroplatus, Tiliqua, Lacerta, Ophiodes, Anguis*)
(1) From cervical ribs only
(*Anolis, Iguana, Crotaphytus, Phrynosoma, Uromastyx, Ceratophora, Calotes, Phrynocephalus, Agama, Pogona,* gekkotans [except *Uroplatus*], *Scincus,* cordylids, *Acanthodactylus,* teiids, varanids, *Shinisaurus, Elgaria, Diploglossus, C. jacksonii, C. vulgaris*).

Character state (0) is probably plesiomorphic for Lepidosauria with character state (1) as a synapomorphy of basal squamates, and secondary reversal in subsets of Acrodonta (*Draco* and *C. chamaeleon*) and other isolated occurrences in taxa (e.g. *Uroplatus*). The feature shows some interspecific variation within genus *Chamaeleo* between states [0] and [1]. The polarity of the character is problematic, but since the muscles come from neck + in both *Sphenodon* and *Caiman*, this is probably the original state with multiple losses of the dorsal rib slips within squamates. A muscle of this type – serratus anterior – exists in mammals (ribs to scapula - e.g. human, Clemente, 1985; Agur et al., 1991; Warfel, 1993; Netter, 1998), and also in birds (serratus superficialis, Berge and Zweers, 1993), but it stems from dorsal (thoracic) ribs.



CHARACTER .12.

13) Presence or absence of deep rib to suprascapula slips

(0) Present
(*Sphenodon*, all Iguania, scincomorphs)
(1) Absent
(*Caiman*, gekkotans, anguimorphs, *Trimeresurus*, *Diplometopon*)

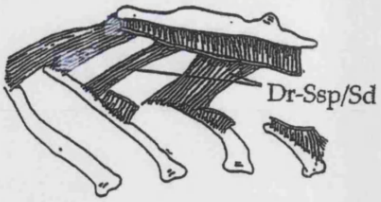
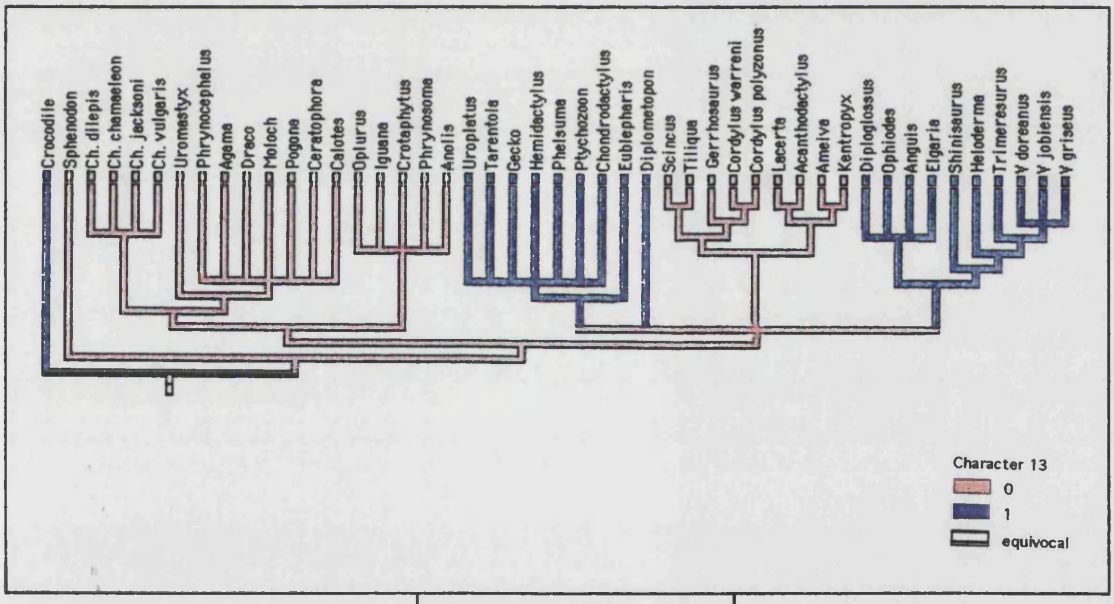


Fig. (10.7.9) *Uromastyx aegyptia* (adult), right dorsal view of the pectoral girdle showing the cervical ribs deep muscle slips to suprascapula/scapulocoracoid (Dr-Ssp/Sd). Scale bar = 1 mm.

Character state (0) is probably plesiomorphic since it is widely distributed (Fig., 10.7.9). Character state (1) is a synapomorphy of anguimorphs and gekkotans, or it may be synapomorphy of Scleroglossa with secondary loss in scincomorphs. This morphological feature may help in strengthening the connection between the ribs and the pectoral girdle. The number of slips shows intraspecific variation, e.g. *Uromastyx aegyptia*.

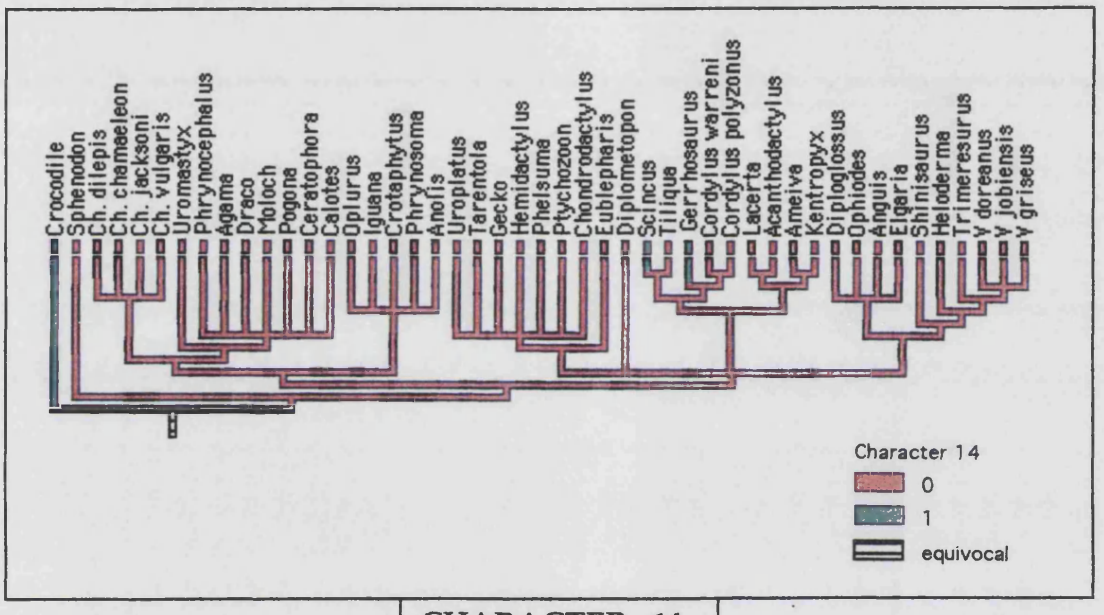


CHARACTER .13.

14) Origin of obliquus capitis

(0) From anterior cervical spines
(most taxa)
(1) From anterior and posterior cervical spines
(*Caiman, Scincus, Gerrhosaurus*)

Since character state (0) is widespread, this is probably primitive. State (1) is found in *Caiman* and in *Scincus* and *Gerrhosaurus*. It would be interesting to look at the distribution of the character state (1) more widely within scincoids (scincids and cordylids), as many authors regard scincids and cordylids as sister taxa (Estes, 1983; Estes et al., 1988; Rieppel, 1988; Evans and Chure, 1998; Hallerman, 1998).



CHARACTER .14.

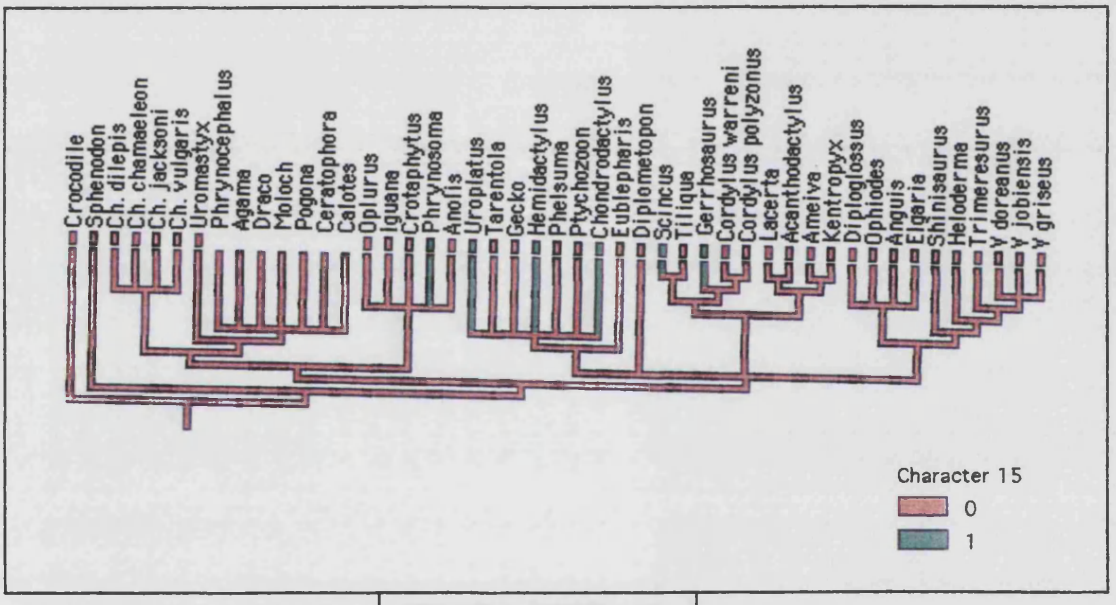
15) Insertion and division of obliquus capitis

(0) One layer on skull
(*Caiman, Sphenodon, Cordylus, Tiliqua,* lacertids, teiids, gekkonids, *Eublepharis,* anguimorphs, chamaeleons, iguanids [except *Phrynosoma*], *Diplometopon, Trimeresurus, Uromastyx*)
(1) Internus and externus branches
(*Scincus, Gerrhosaurus, Hemidactylus, Uroplatus, Chondrodactylus, Phrynosoma*)

Note: The muscle was not investigated in agamids.

Character state (0) is plesiomorphic, while state (1) is an interesting character with a problematic random distribution. The seemingly random distribution of this character state raises the possibility of a functional explanation, but there is no obvious similarity in their ecology. *Scincus* is an African sand-swimmer that

moves very fast in loose sand (no tunnel formation) (Bauer, 1992); the plated lizard *Gerrhosaurus* (sub-Saharan African or Madagascar) inhabits rocks or sometimes sand dunes (Zug, 1993); the gecko *Hemidactylus* is terrestrial to arboreal, with adhesive feet for fast climbing (Bellairs, 1969); *Uroplatus* (gekkonid) is a tree climber from Madagascar (Zug, 1993); and the horned lizard *Phrynosoma* (iguanid) is a slow moving ant-feeding specialist which digs burrows and covers itself with sand (Bauer, 1992). Herrel and De Vree (1999) described the division of rectus and obliquus capitis in *Heloderma horridum* into deep and superficial layers.



CHARACTER .15.

16) Insertion of obliquus capitis

(0) Paroccipital process
(*Caiman, Sphenodon, Shinisaurus*, gekkonids, *Diplometopon, Trimeresurus, Eublepharis*, cordylids, lacertids, teiids, *Tiliqua,*, varanids, anguids, iguanids, chamaeleons)
(1) Paroccipital process and quadrate
(*Uroplatus*)
(2) Paroccipital process and skull roof
(*Scincus*)

Note: In agamids the muscle was not investigated. Character state (0) is widely

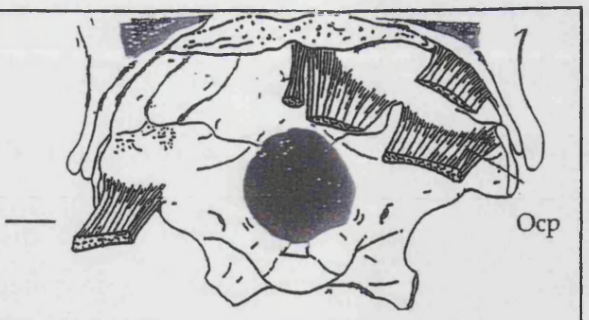
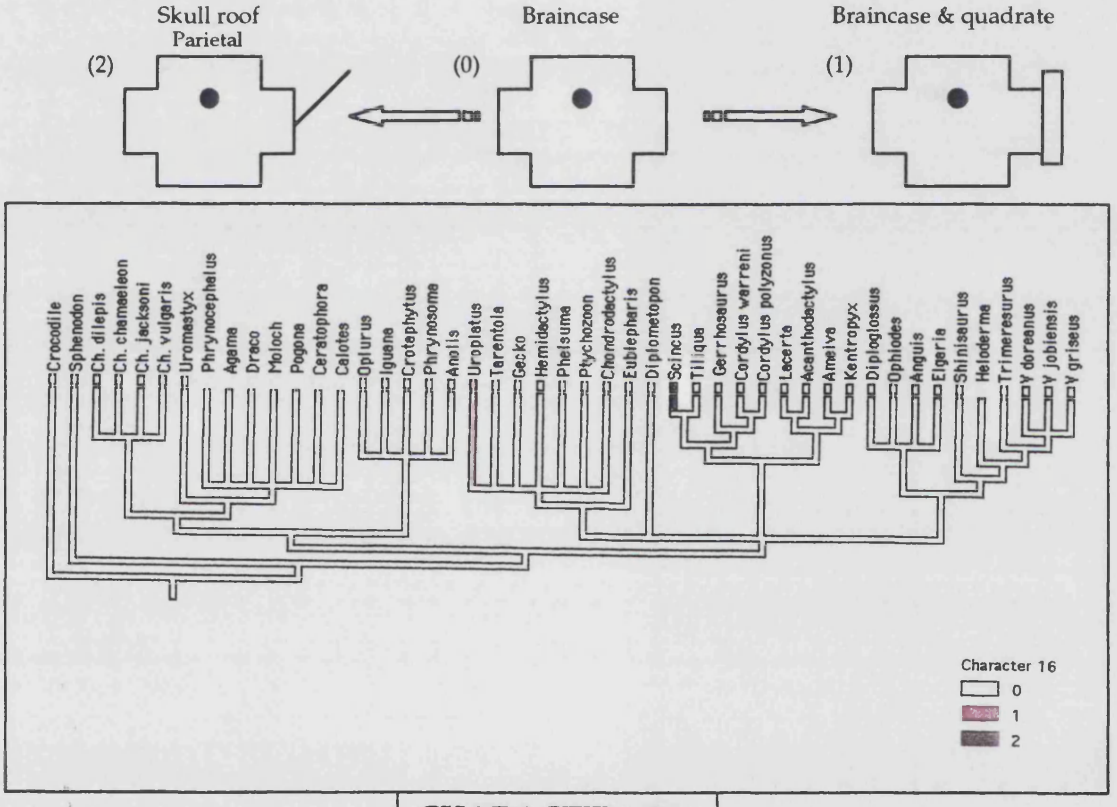


Fig. (10.7.10) *Shinisaurus crocodilurus*, occipital view of the skull showing the insertion of obliquus capitis (Ocp) on the paroccipital process. Scale bar = 1 mm.

distributed and probably plesiomorphic (Fig., 10.7.10). Derived states are found in the specialised *Uroplatus* (1) and in *Scincus* (2). More scincids need to be dissected.



CHARACTER .16.

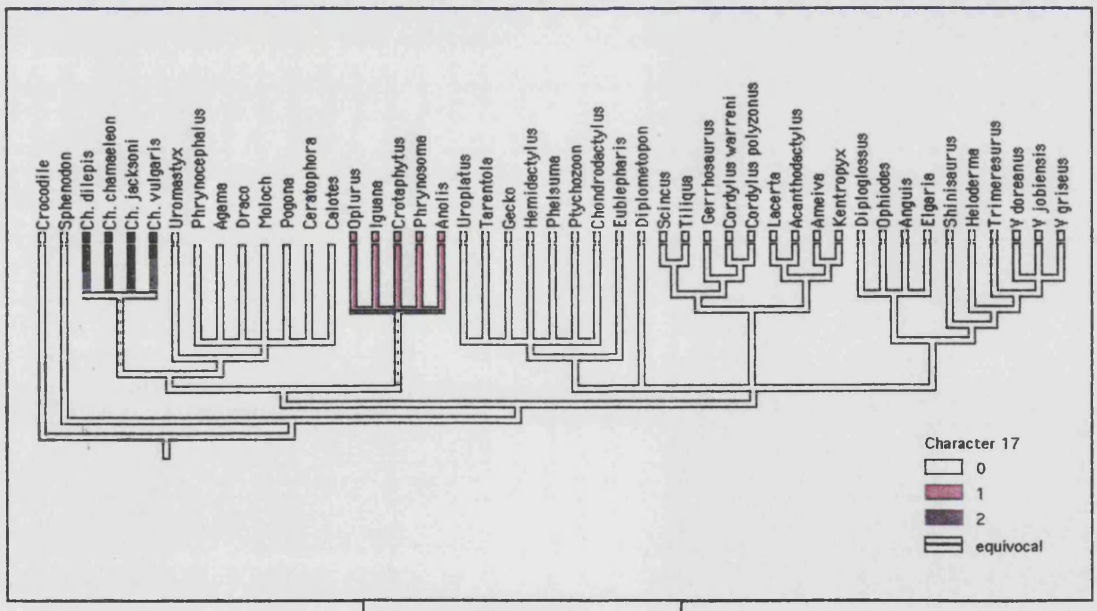
17) Insertion of splenius capitis

(0) Parietal
(most groups [except iguanians], including *Uromastyx*)
(1) Parietal + supraoccipital
(iguanids)
(2) Supraoccipital (chamaeleons)

Note: In agamids the muscle was not investigated.

Character state (0) is plesiomorphic. The extension of the muscle towards the supraoccipital appears to be a synapomorphy of the iguanids dissected (1). Herrel and De Vree (1999) reported the insertion of the splenius capitis on the parietal and supraoccipital in *Heloderma horridum*. Character state (2) in *Chamaeleo* limits the attachment to the supraoccipital (more dissection is needed of other genera).

In chamaeleons, the reduction of the parietal and the elevation of the squamosal (casque) precludes muscle attachment to the parietal, leaving just the supraoccipital and crista parietalis inferior. This muscle, with others, assists in fixing the head on the neck rather than elevation of the head. Clearly this muscle needs to be studied in agamids.



CHARACTER .17.

18) Branching of splenius capitis before insertion on the skull

(0) Undivided
(*Caiman, Sphenodon*, gekkotans, *Heloderma, Ophiodes*, scincomorphs, *Trimeresurus, Diplometopon*, chamaeleons, *Phrynosoma, Uromastyx, Ceratophora, Pogona*)
(1) Branched – slip on longissimus capitis 1
(varanids, *Shinisaurus*, iguanids [except *Phrynosoma*])

Note: In most agamids and anguids the muscle was not investigated.

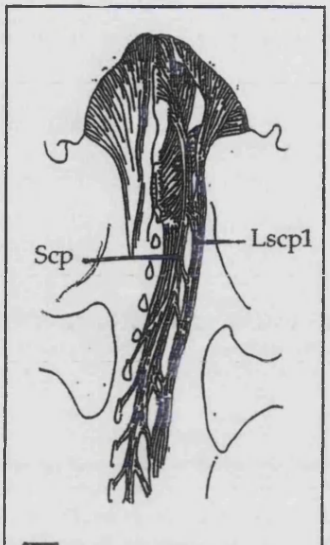
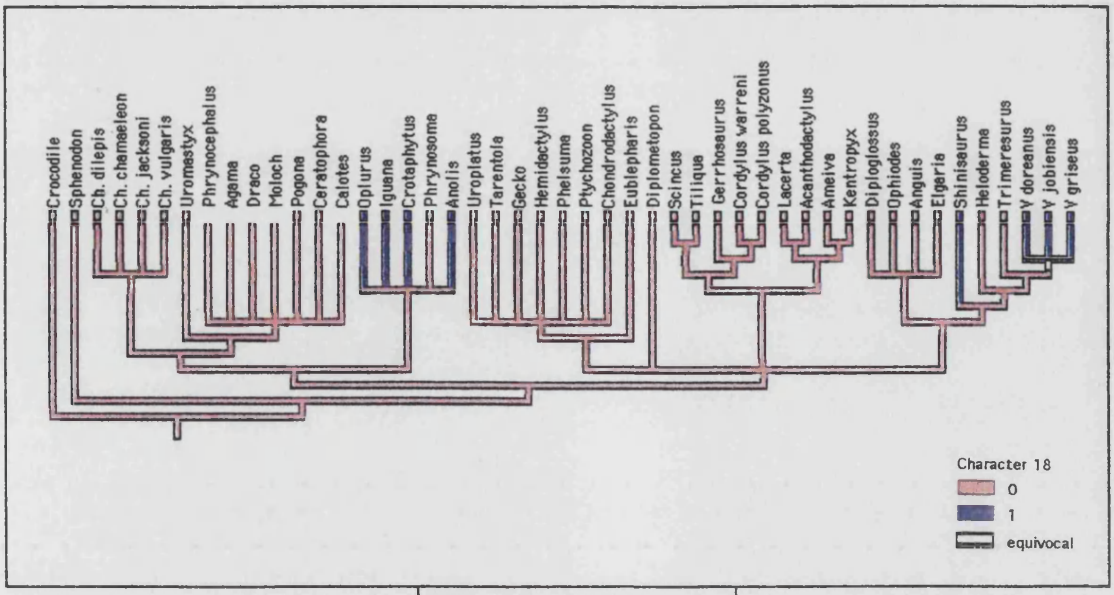


Fig. (10.7.11) *Oplurus cyclurus*, Dorsal view of the craniocervical region showing branches of splenius capitis (Scp) on longissimus capitis 1 (Lscp1) muscle. Scale bar = 1 mm.

Character state (0) is widespread and seems plesiomorphic. Character state (1) may be a synapomorphy of iguanids with reversal in *Phrynosoma*, but the muscle in agamids was not investigated, and it may be an iguanian apomorphy. Within Scleroglossa it is limited to varanids and *Shinisaurus* (it would be interesting to dissect *Xenosaurus*). This character is present in some iguanids and anguimorphs but without an obvious phylogenetic pattern (Fig., 10.7.11). Branching of the splenius capitis conceivably assists in the connection and reinforcement of the craniocervical muscles.



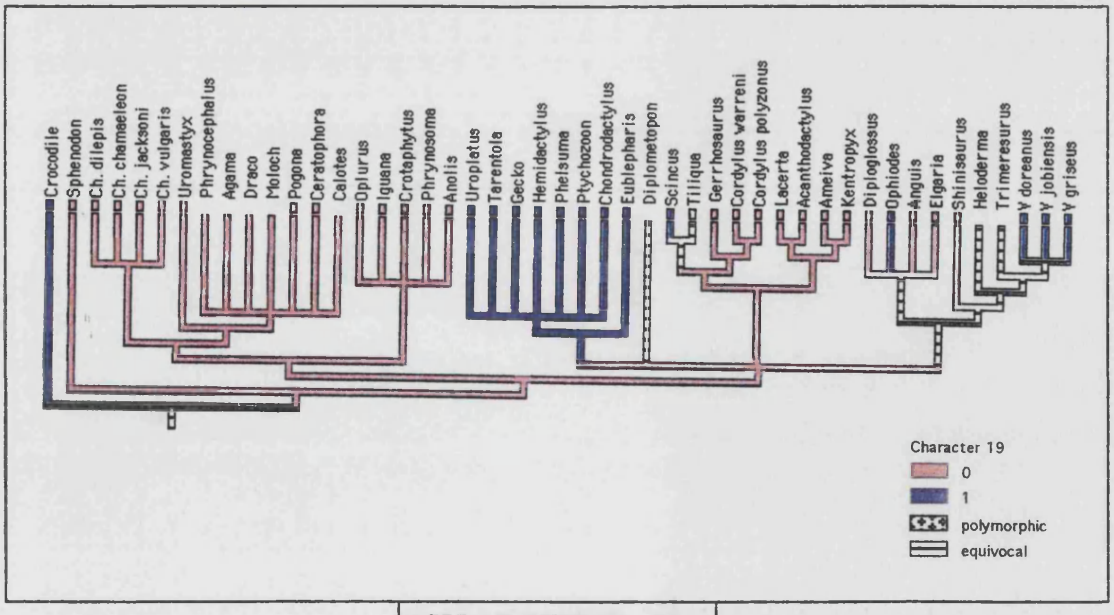
CHARACTER .18.

19) Splenius capitis extension

(0) Superficial to cervical and dorsal neural spines
(*Sphenodon*, cordylids, lacertids, teiids, iguanids, most chamaeleons, *Uromastyx*, *Pogona*, *Ceratophora*, *Shinisaurus*, most anguids [except *Ophiodes*], *Tiliqua nigrolutea*)
(1) Superficial to cervical spines only
(*Caiman*, gekkotans, *Tiliqua rugosa*, *Scincus*, varanids, *Ophiodes*)

Note: In *Diplometopon* and *Trimeresurus* and most agamids the muscle were not investigated.

Character state (0) is probably plesiomorphic. Character state (1) may be a synapomorphy of gekkotans (for which monophyly is universally supported e.g. McDowell and Bogert, 1954; Underwood, 1954; Kluge, 1967; Estes, 1983; Estes et al., 1988), but it arises independently in varanids and *Ophiodes*. The character shows interspecific variation in *Tiliqua* between two states [0] and [1], which decreases its phylogenetic value. Bearing in mind Lee's (1998) suggesting that xantusiids are related to gekkotans, it would be interesting to investigate this muscle in the group. Unfortunately, no xantusiid material was available for this project.



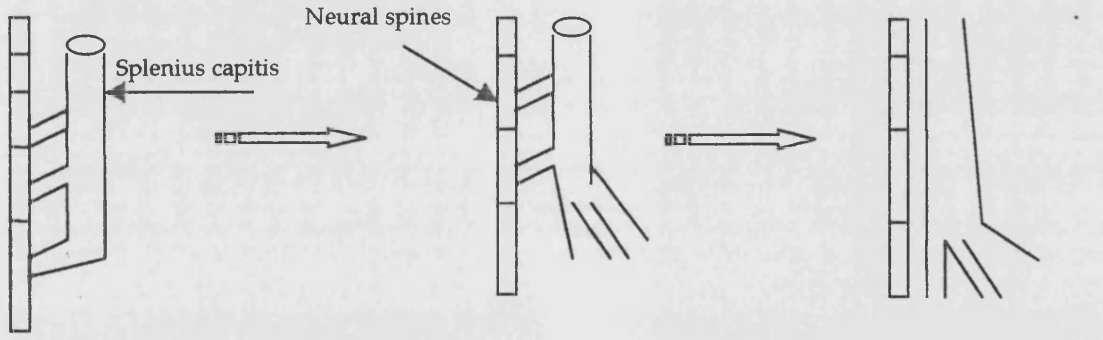
CHARACTER .19.

20) Origin of splenius capitis

(0) Centrally from the neural spines
(*Sphenodon*, scincomorphs, *Trimeresurus*, *Phrynosoma*, *Uromastyx*, *Ceratophora*, *Pogona*, chamaeleons)
(1) Centrally from neural spines and laterally from muscle fascia of longissimus dorsi and iliocostalis
(*Caiman*, most iguanids [except *Phrynosoma*], *Eublepharis*)
(2) Above neural spines and laterally from muscle fascia
(gekkonids, anguimorphs, *Diplometopon*)

Note: In most agamids the muscle was not investigated.

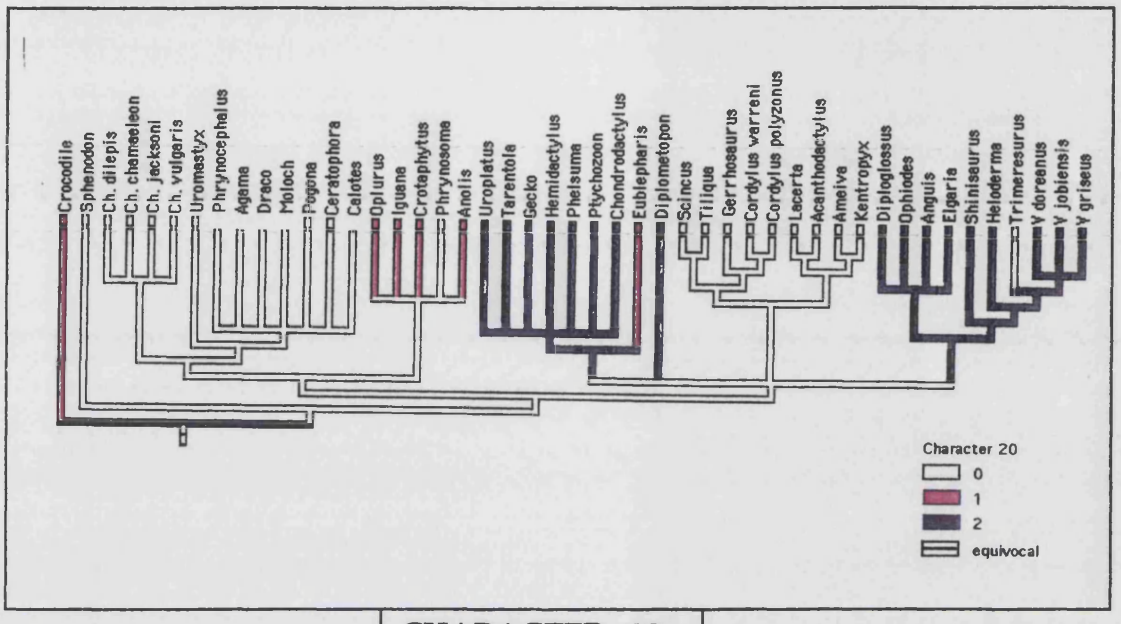
Character state (0) is plesiomorphic. Character state (1) may be a synapomorphy of iguanids (except *Phrynosoma*), although many agamids were not examined (for this feature, the presence of state (0) in *Uromastyx* as well in *Ceratophora*, *Pogona* and chamaeleons suggests a difference between iguanids and acrodonts). Character state (2) is a synapomorphy of anguimorphs and gekkotans with the exception of eublepharids and therefore probably arose independently in the two groups.



Dorsal view of the cervical and dorsal spines showing the way splenius capitis originates from the spines and/or muscle fascia in reptiles.

The character appears to show an evolutionary trend towards the gradual movement of muscle slips from spines towards muscle fascia, particularly in

iguanids, gekkotans and anguimorphs. Interestingly gekkotans, anguimorphs and *Diplometopon* share the same derived character state.



CHARACTER .20.

21) Presence or absence of spinalis capitis

(0) Absent
(*Caiman, Sphenodon*, scincomorphs, *Trimeresurus*, iguanids, *Uromastyx*, chamaeleons, *Diplometopon, Ophiodes*)
(1) Present
(varanids, *Shinisaurus*, gekkotans)

Note: In most agamids, *Heloderma, Elgaria* and *Diploglossus* the muscle was not investigated.

Character state (0) appears plesiomorphic. The absence of the muscle in *Caiman, Sphenodon* and the iguanians studied, suggests its presence (1) may be a scleroglossan synapomorphy, but its absence in most scincomorphs is problematic.

Either it was lost independently (reversal) or (1) is a character of gekkotans and

some anguimorphs. When spinalis capitis is present, it runs from the cervical neural spines and extends deep to splenius capitis to attach to the parietal (Fig., 10.7.12). It either originates from the anterior (e.g. varanids) or posterior (e.g. *Shinisaurus*, gekkotans) cervical spines.

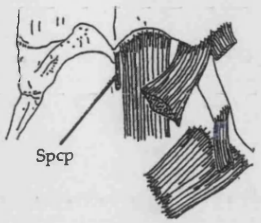
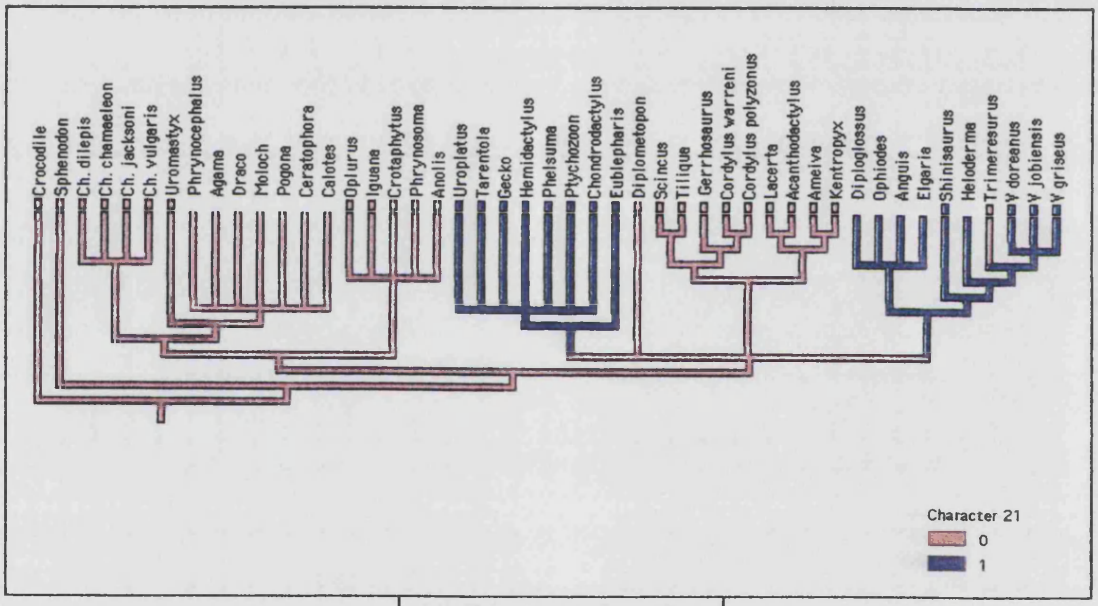


Fig. (10.7.12) *Gekko gecko*, dorsal view of the skull showing the insertion of spinalis capitis (Spcp) on the parietal. Scale bar = 1mm.



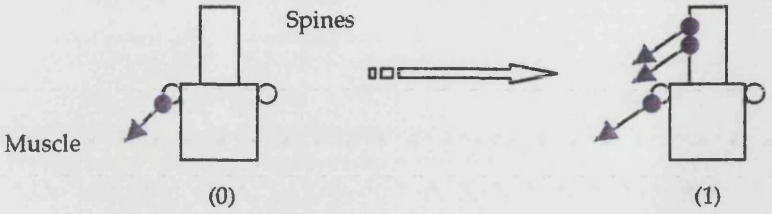
CHARACTER .21.

22) Insertion of longissimus dorsi

(0) Lower lateral surface of anterior zygapophyses
(most taxa)
(1) Anterior zygapophyses and neural spines
(*Scincus*)

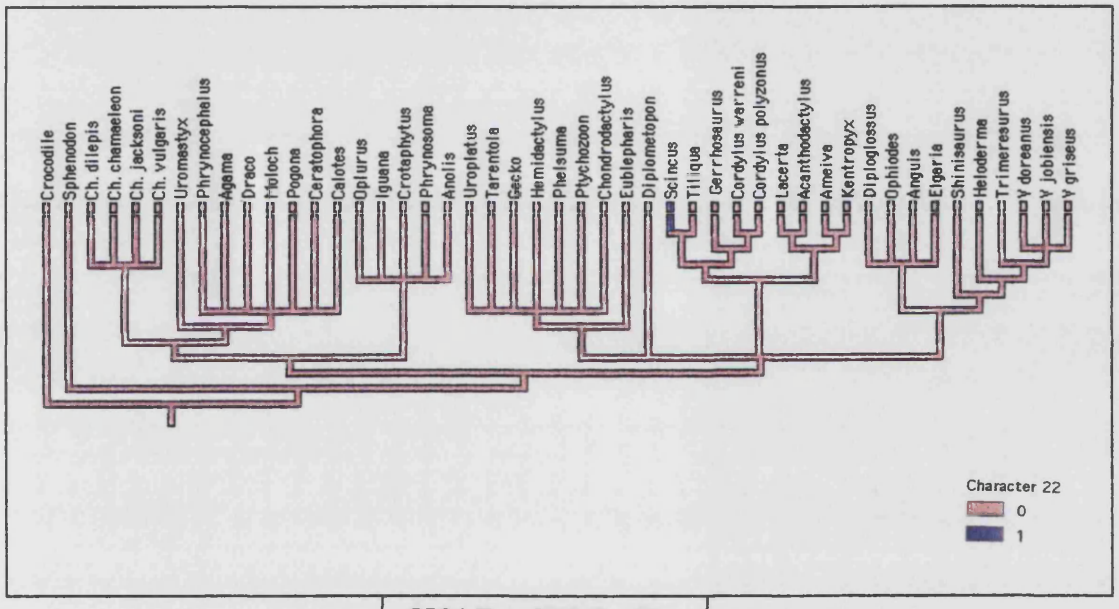
In all but one of the taxa examined, the muscle inserts on the lower lateral surface of the zygapophyses as it extends anteriorly along the vertebral column

(plesiomorphic state [0]). In *Scincus,* however a dorsal extension of the attachment occurs towards the spines of the anterior vertebrae; this is one of a number of special features seen in this genus (1).



Left lateral view of vertebrae showing the attachment of the longissimus dorsi on the zygapophyses and spines.

Clearly, however, more dissection of scincids is needed.

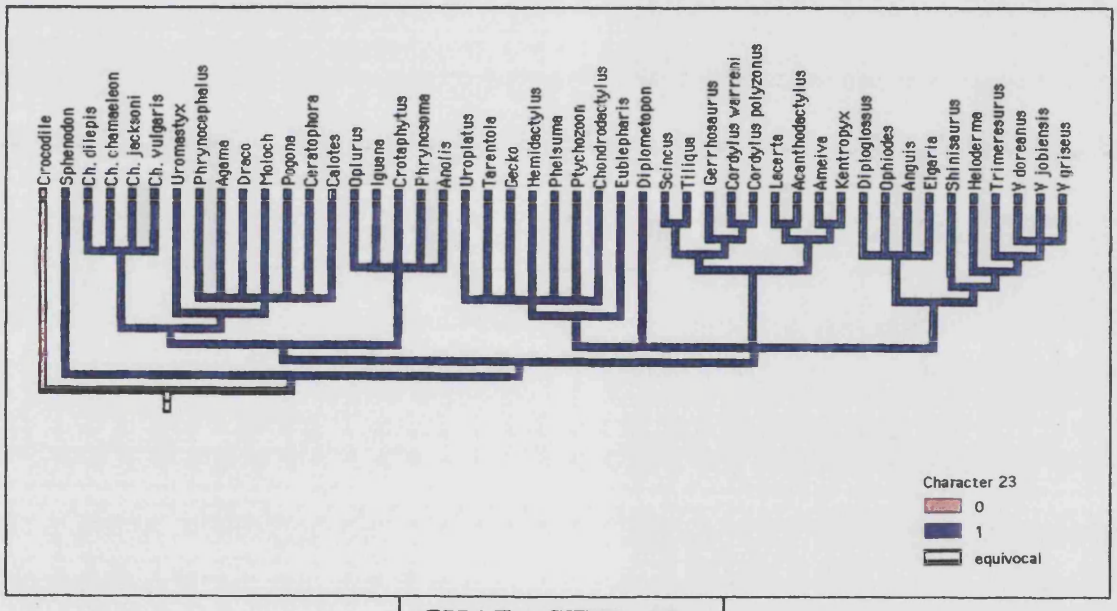


CHARACTER .22.

23) Presence or absence of longissimus capitis 1

(0) Absent
(*Caiman*)
(1) Present
(all lepidosaurs)
(Polarity uncertain)

Longissimus capitis branches are the cervicus extension of the longissimus dorsi (Herrel and De Vree, 1999), and longissimus capitis 1 is the dorsal branch. Character state (1) is present in all lepidosaurs, but is absent in *Caiman* (0). Berge and Zweers (1993) do not described an equivalent muscle in birds, while in mammals (Filan, 1990), including humans (Clemente, 1985; Agur et al., 1991; Warfel, 1993; Netter, 1998), there is only one branch of longissimus capitis that inserts laterally on the mastoid (=paroccipital) bone (~ longissimus capitis 2). So the possession of longissimus capitis 1 that inserts dorsally on the parietal may be a synapomorphy of lepidosaurs.



CHARACTER .23.

24) Insertion of longissimus capitis 1

(0) As one branch on the skull
(most lepidosaurs)
(1) As two branches
(Diplometopon)

The muscle usually inserts as one bundle on the skull (0), but it divides into

two branches in *Diplometopon* (parietal and otic capsule) (1). The condition is most striking in *Diplometopon* and needs to be examined in a wider range of amphisbaenians. Potentially, its more complex structure could be related to head movements during burrowing (Fig., 10.7.12).

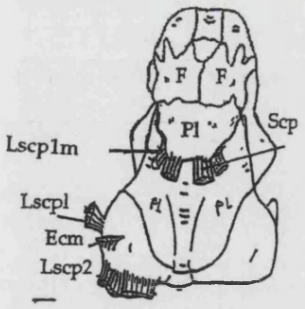
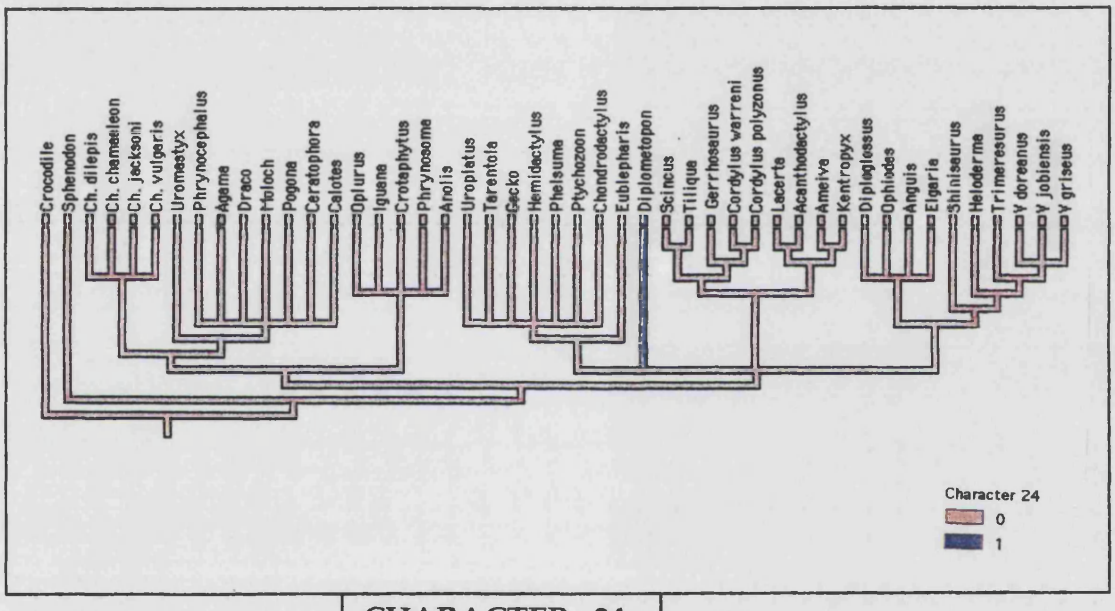


Fig. (10.7.13) *Diplometopon*, dorsal view of the skull showing the two insertions of longissimus capitis 1 (Lscp1m &Lscp1l) on the occipital region. Scale bar = 1 mm.



CHARACTER .24.

25) Position of the insertion of longissimus capitis 1

(0) On parietal +/- squamosal or supratemporal
(most groups)
(1) On parietal and otic capsule (or paroccipital process)
(*Phrynosoma, Diplometopon*)
(2) On supraoccipital
(chamaeleons)

The muscle usually inserts on the skull roof and sometimes lateral skull components (0). The insertion shifts ventrally towards the otic capsule in

Diplometopon, or paroccipital process in *Phrynosoma* (1) (Fig., 10.7.14). In chamaeleons, the parietal is reduced and all the muscles that primitively insert on the parietal move ventrally onto the supraoccipital, including longissimus capitis 1 (2). However, this needs to be examined in more basal chamaeleons (*Brookesia, Bradypodion*), and in agamids.

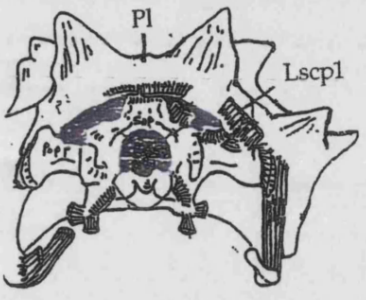
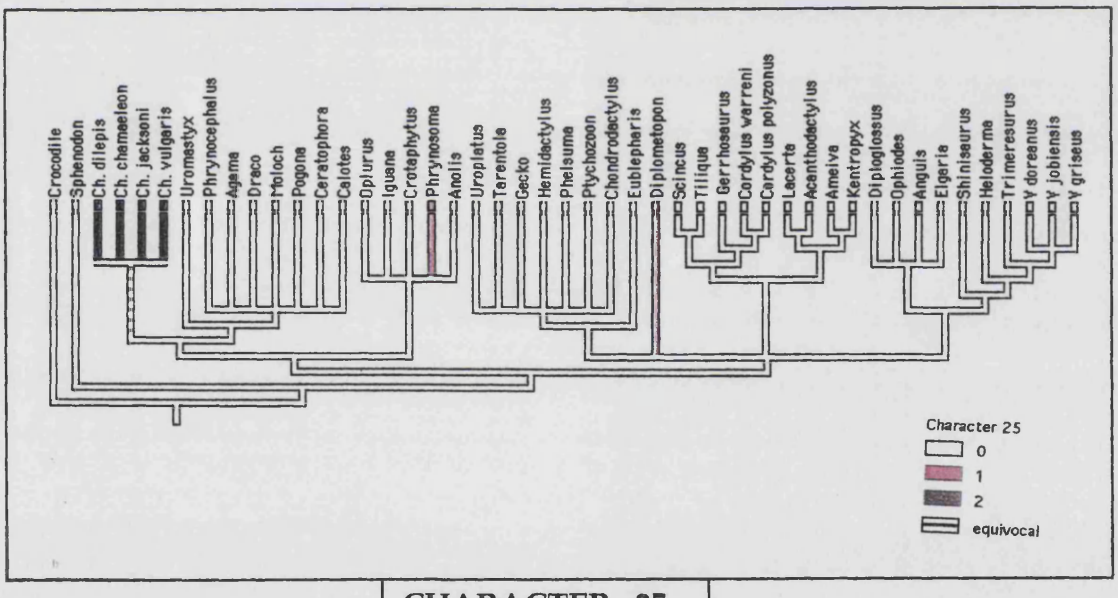


Fig. (10.7.14) *Phrynosoma platyrhinos*, occipital view of the skull showing the insertion of the longissimus capitis 1 (Lscp1) on the parietal & paroccipital process. Scale bar = 1 mm.



CHARACTER .25.

26) Shape of insertion of longissimus capitis 1.

(0) As a flat narrow end
(most groups)
(1) As a wide triangular area on the posterolateral side of the parietal
(Gekkota)

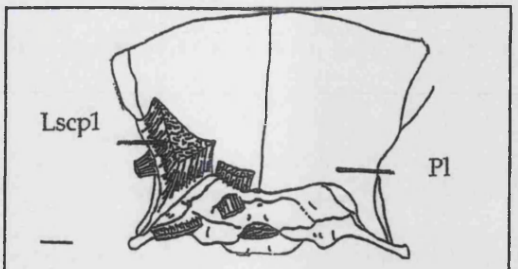
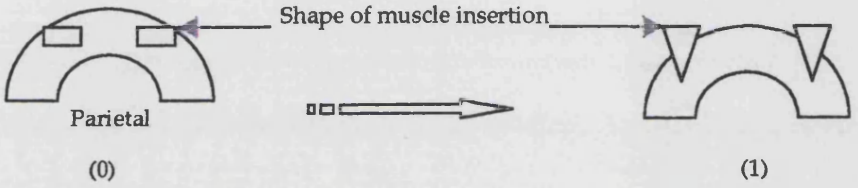
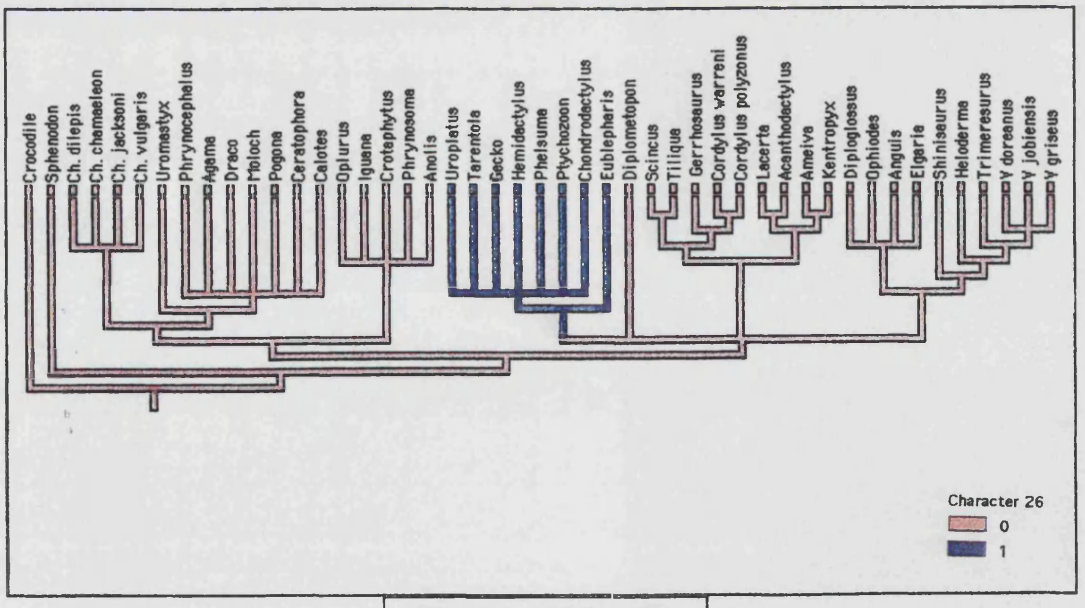


Fig. (10.7.15) *Hemidactylus flaviviridis.* posterodorsal view of the skull showing the triangular insertion of longissimus capitis 1 (Lscp1). Scale bar = 1 mm.

The muscle usually inserts on the skull as a flat bundle (0), but in all gekkotans it inserts on the parietal as a thick triangular mass (1) (Fig., 10.7.15).



Character state [1] is a distinctive gekkotan feature.



CHARACTER .26.

27) Insertion of longissimus capitis 2

(0) On paroccipital process
(*Caiman, Sphenodon, Diplometopon*, gekkotans, anguimorphs, iguanids [except *Phrynosoma*], agamids)
(1) On skull roof +/- paroccipital process
(scincomorphs [L-shaped], chamaeleons)
(2) On oto-occipital
(*Trimeresurus*)
(3) Absent
(*Phrynosoma*)

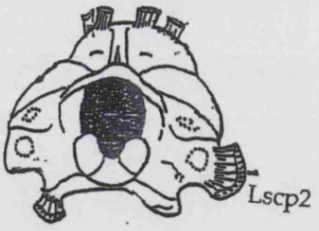
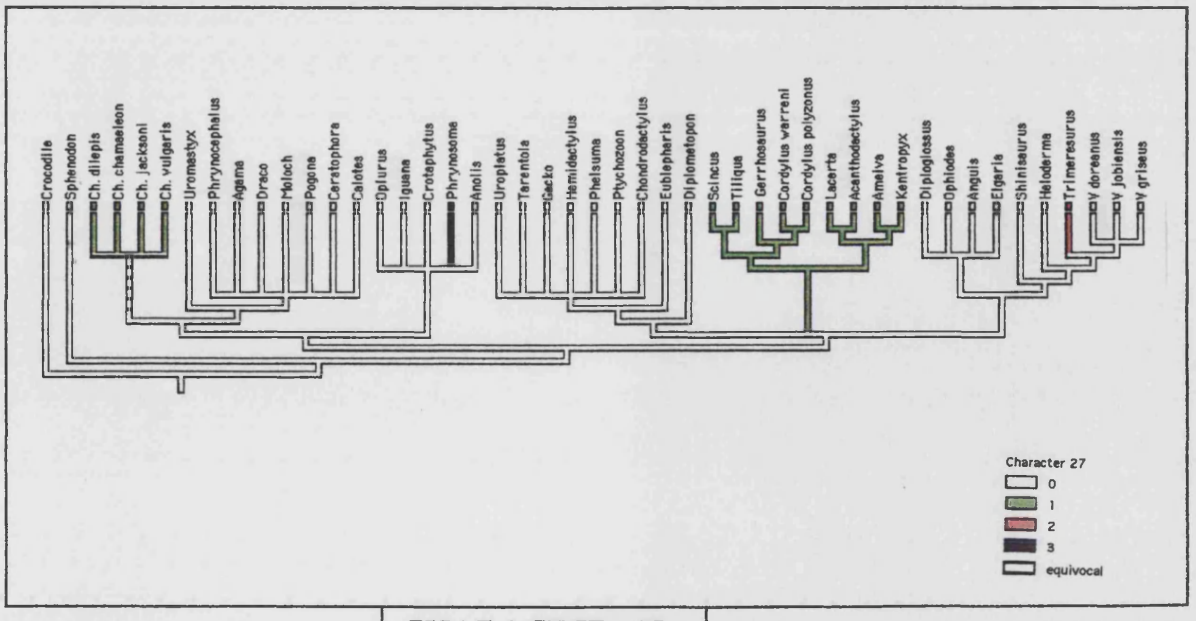


Fig. (10.7.16) *Diplometopon zarudnyi*, occipital view of the skull showing the insertion of longissimus capitis 2 (Lscp2) on the paroccipital process. Scale bar = 1 mm.

The muscle usually inserts on the paroccipital process (0) (Fig., 10.7.16), as in mammals where the homologous muscle inserts on the mastoid process (Clemente, 1985; Filan, 1990; Agur et al., 1991; Warfel, 1993; Netter, 1998). The insertion has shifted onto the oto-occipital close to the supraoccipital in *Trimeresurus* (2), while the muscle extends laterally towards the skull roof in scincomorphs and chamaeleons (1). In *Phrynosoma* the muscle is absent (3). Character state (1) shows interspecific variation within *Chamaeleo* (skull roof and paroccipital, *C. chamaeleon, C. vulgaris, C. dilepis; C. jacksonii* on skull roof only). More dissections are needed to check the distribution of the derived characters.



CHARACTER .27.

28) Presence or absence of longissimus capitis 3

(0) Present
(*Sphenodon*, chamaeleons, *Iguana*)
(1) Absent
(*Caiman*, other squamates)

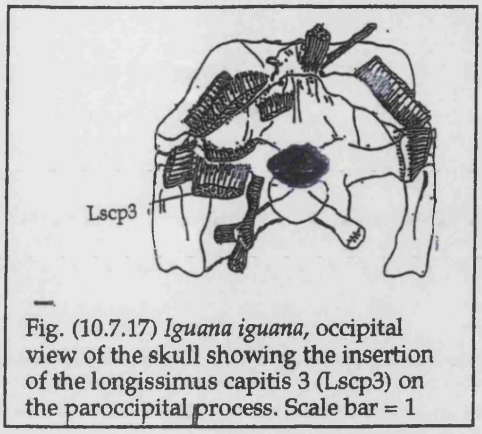
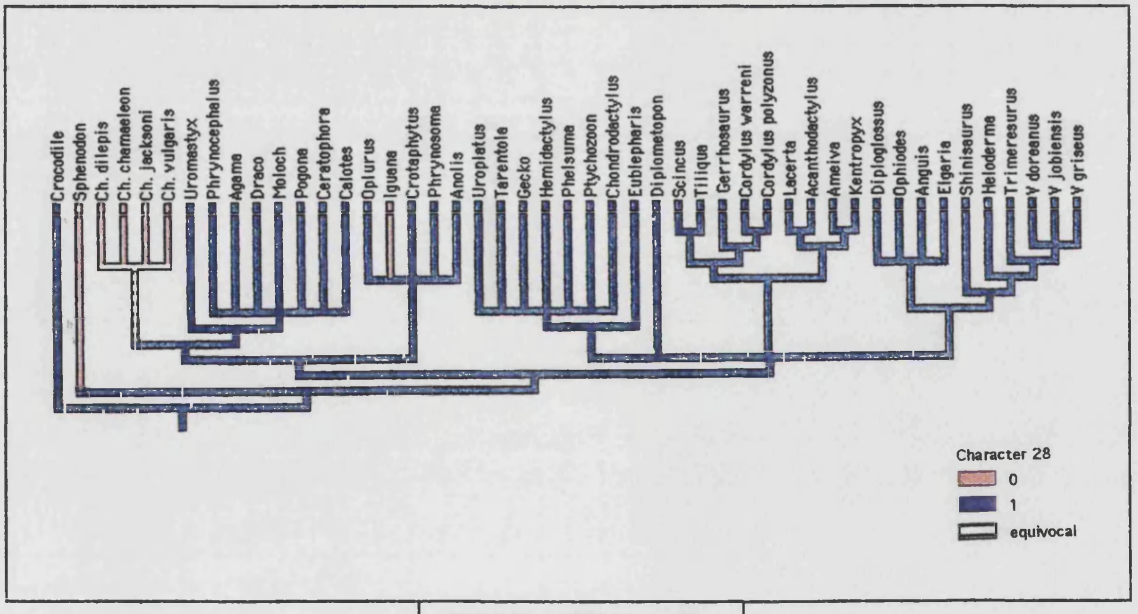


Fig. (10.7.17) *Iguana iguana*, occipital view of the skull showing the insertion of the longissimus capitis 3 (Lscp3) on the paroccipital process. Scale bar = 1

There are two alternatives: character state (0) is primitive and then state (1) has arisen several times (less parsimonious); or character state (1) is primitive on the basis of its wider distribution. In this case, an additional muscle slip has arisen in *Sphenodon*, chamaeleons and *Iguana* (Fig., 10.7.17). Further dissection, especially of agamids (in *Uromastyx* the muscle was absent as in state [1]) and turtles, would help to decide the primitive condition.

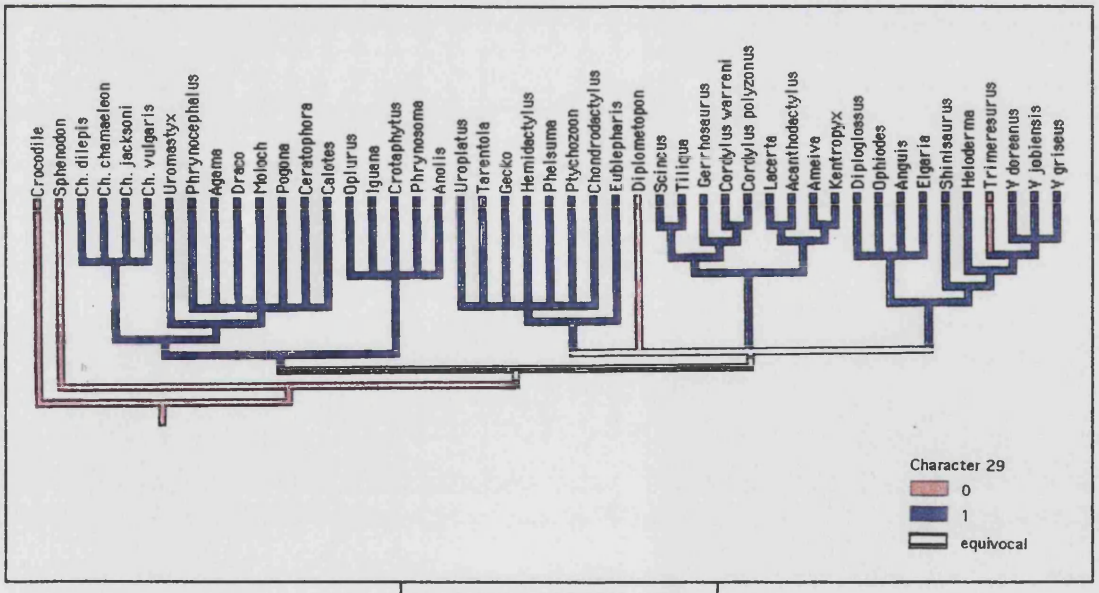


CHARACTER .28.

29) Presence or absence of longissimus capitis minor

(0) Absent
(*Caiman, Sphenodon, Trimeresurus, Diplometopon*
(1) Present
(iguanians, gekkotans, scincomorphs, anguimorphs)

Both longissimus capitis 4 and minor (= lateral vertebral muscle) assist in lateral bending of the neck (Wahba et al., 1992c). This muscle is absent in *Sphenodon* and *Caiman* (0), but present in all squamates (1) except *Trimeresurus* and *Diplometopon*. The probable explanation is that the presence of the muscle is derived for squamates with secondary loss in snakes and amphisbaenians. More dissections of snakes and amphisbaenians are needed. In some mammals a homologous muscle (rectus capitis lateralis) is present and originates from the atlas transverse process to insert ventrally on the mastoid behind the auditory meatus (Filan, 1990). This suggests that state (1) could be the primitive condition, but dissections are needed of turtles.



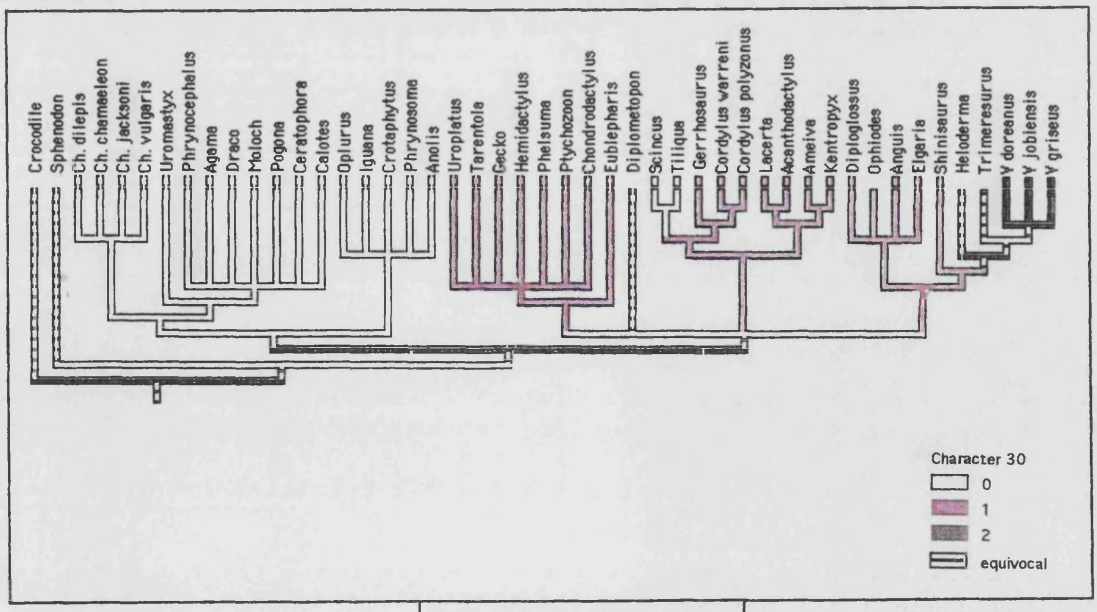
CHARACTER .29.

30) Insertion of longissimus capitis minor when present

(0) On basioccipital (+/- adjacent oto-occipital)
(scincids, iguanians)
(1) On the lateral margin of the oto-occipital (includes crista tuberalis)
(gekkotans, *Shinisaurus*, cordylids, lacertids, teiids, anguids)
(2) On or close to the paroccipital process
(varanids)

Fig. (10.7.18) *Scincus miternus*, occipital view of the skull showing the insertion of longissimus capitis minor (Lscpm) on the basioccipital. Scale bar = 1 mm.

Primitively, the muscle inserts on the basioccipital and oto-occipital where present (iguanians and scincids) (0), or the oto-occipital only (including crista tuberalis) (1). In varanids, it is shifted further dorsally to insert on the oto-occipital close to the paroccipital process (2). Because this muscle is absent in *Sphenodon* and *Caiman*, the character is difficult to polarize – either state (0) or (1) could be primitive for squamates. If (0), then (1) arose at the base of Scleroglossa with a reversal in scincids (Fig., 10.7.18). If (1), then (0) are an iguanian synapomorphy, also found in scincids. Dissection of a greater range of scincids might help to resolve this.

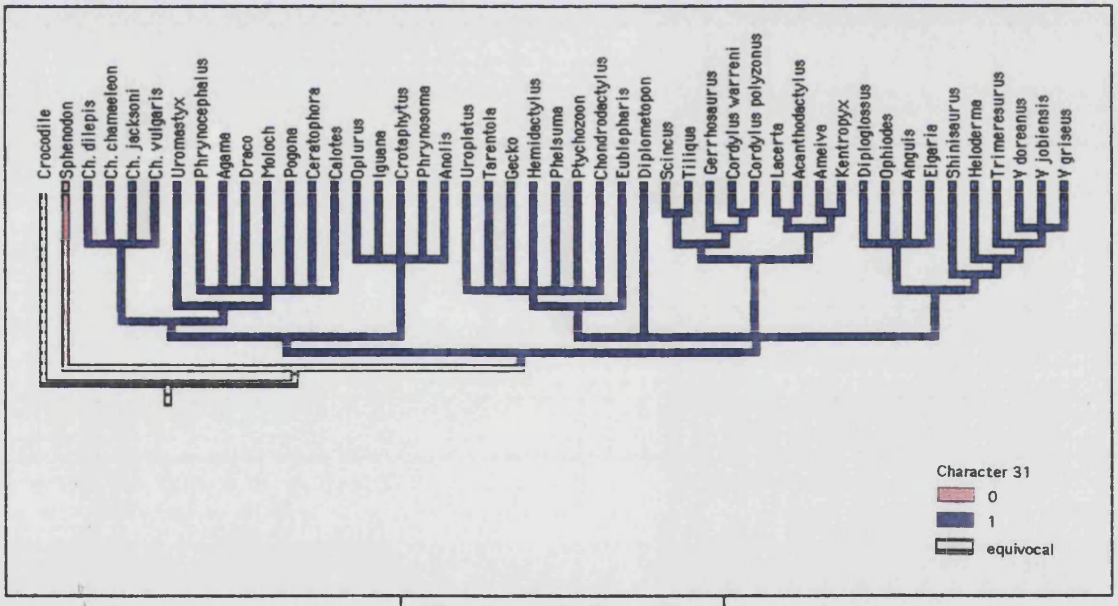


CHARACTER .30.

31) Insertion of longissimus cervicus

(0) Separate branches on atlas and proatlas
(*Sphenodon*)
(1) One branch on atlas
(*Caiman*, squamates)

Romer (1956) reported the presence of the proatlas in *Sphenodon*, crocodiles and chamaeleons. I found no evidence of a proatlas in chamaeleons and did not investigate the proatlas in *Caiman*. In all squamates examined, the muscle inserts as one bundle on the atlas (1). In *Sphenodon* it divides to send an extra slip to the proatlas (0), absent in squamates. Character state (1) is found in all squamates with loss of proatlas, but also in *Caiman*. Further examination of a wider range of crocodiles is needed.

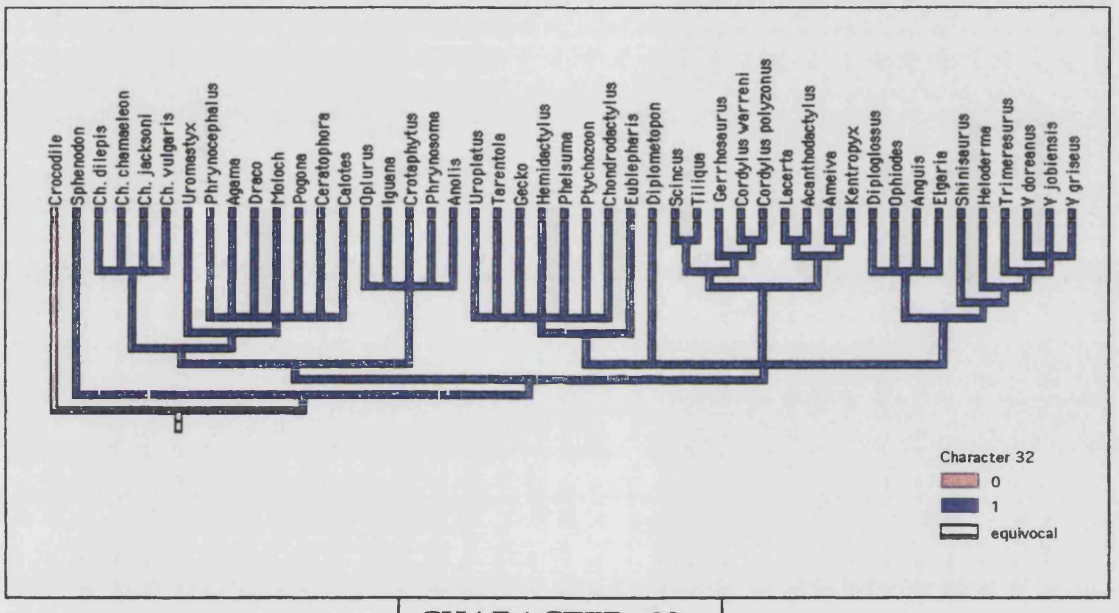


CHARACTER .31.

32) Insertion of iliocostalis cervicus

(0) On atlas rib and muscle fascia of longus colli
(*Caiman*)
(1) On atlas transverse process
(all lepidosaurs)

In lepidosaurs, the muscle inserts on the atlas transverse process (1), but in *Caiman* it attaches to the distal end of the atlas rib (0) (Cleuren and De Vree, 2000). Further dissections of crocodiles might help to determine the polarity. Note: In *Phrynosoma* the skull insertion is divided into two parts (dorsalis + ventralis). The homologies of this muscle are problematic in birds, and the situation in mammals and birds is complicated because the cervical ribs are fused to vertebrae (Zusi, 1985; Filan, 1990; Berge and Zweers; 1993).



CHARACTER .32.

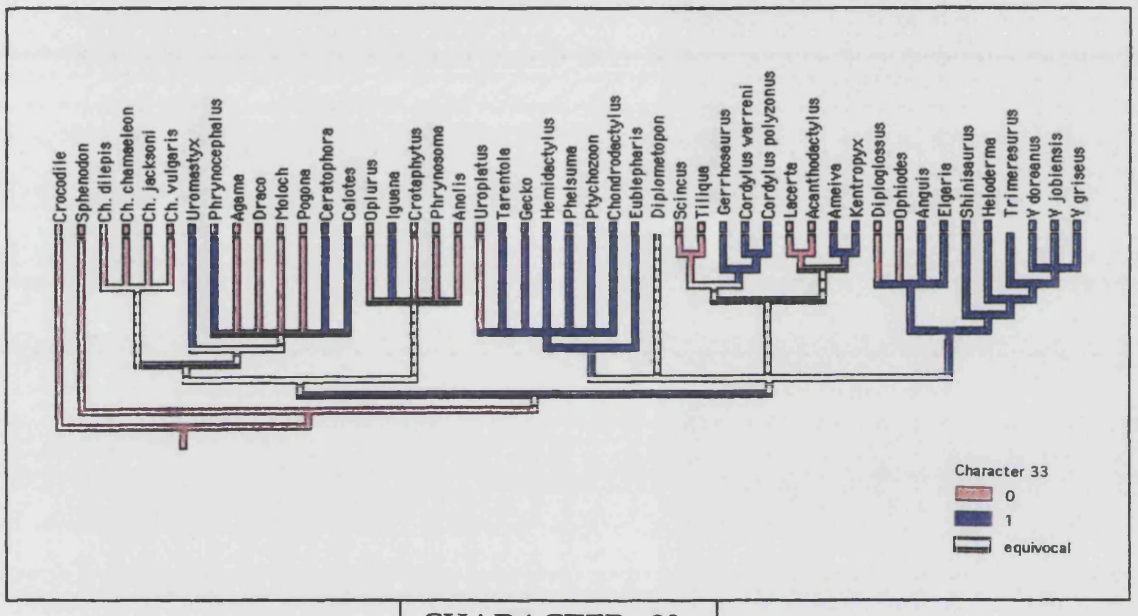
33) Origin of longus colli (a)

(0) From dorsal vertebrae
(*Caiman, Sphenodon,* iguanids [except *Iguana*], *Uroplatus,* lacertids, *Diploglossus, Ophiodes,* chamaeleons, *Moloch, Draco, Pogona, Agama, Scincus, T. nigrolutea*)
(1) From cervical vertebrae only (+/- D 1)
(most gekkotans, teiids, cordylids, varanids, *Heloderma, Shinisaurus, Elgaria, Anguis, Iguana, Uromastyx, Calotes, Ceratophora, Phrynocephalus, T. rugosa*)

Note: In *Diplometopon* and *Trimeresurus* the cervical vertebrae cannot be differentiated.

From the distribution state (0) could be plesiomorphic (also found in mammals [Penning, 1968]), while state (1) may have arisen at the base of squamates (also in birds [Berge + Zweers, 1993]). Alternatively, state (1) is a scleroglossan feature that has arisen independently in some iguanians.

However, it is a very variable character without clear pattern of distribution and shows interspecific variation (e.g. *Tiliqua nigrolutea* [0], *T. rugosa* [1]).



CHARACTER .33.

34) Origin of longus colli (b)

(0) From intercentra/hypapophyses (+/- rib ligaments)
(*Sphenodon*, *Caiman*, gekkonids [intercentra + rib ligaments].
Varanids and *Trimeresurus* [hypapophyses])
(1) From centra (+/- rib ligaments)
(chamaeleons, *Eublepharis*, scincids, cordylids, lacertids,
teiids, *Heloderma*, *Shinisaurus*, anguids, iguanids,
agamids, *Diplometopon*)

The muscle originates from intercentra or centra (+/- rib ligament), but with a clearer distribution pattern. *Caiman* and *Sphenodon* shows what is presumably the primitive state (0). The advanced state (origin from centra [1]) is found in

most squamates (Fig., 10.7.19), except gekkonids and varanids. Since eublepharids show state (1), secondary reversal presumably occurred in the amphicoelous gekkonids. Interestingly, this character brings varanids and *Trimeresurus* together (origin and extension of longus colli from hypapophyses), presumably due to the extra development of the intercentra (hypapophyses).

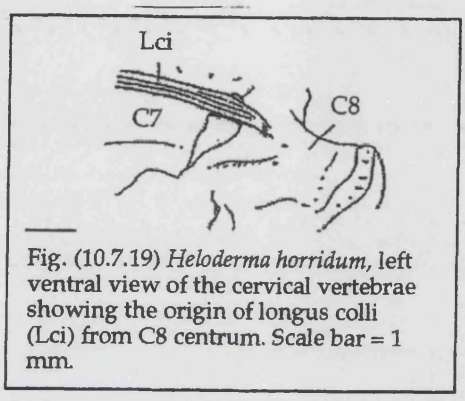
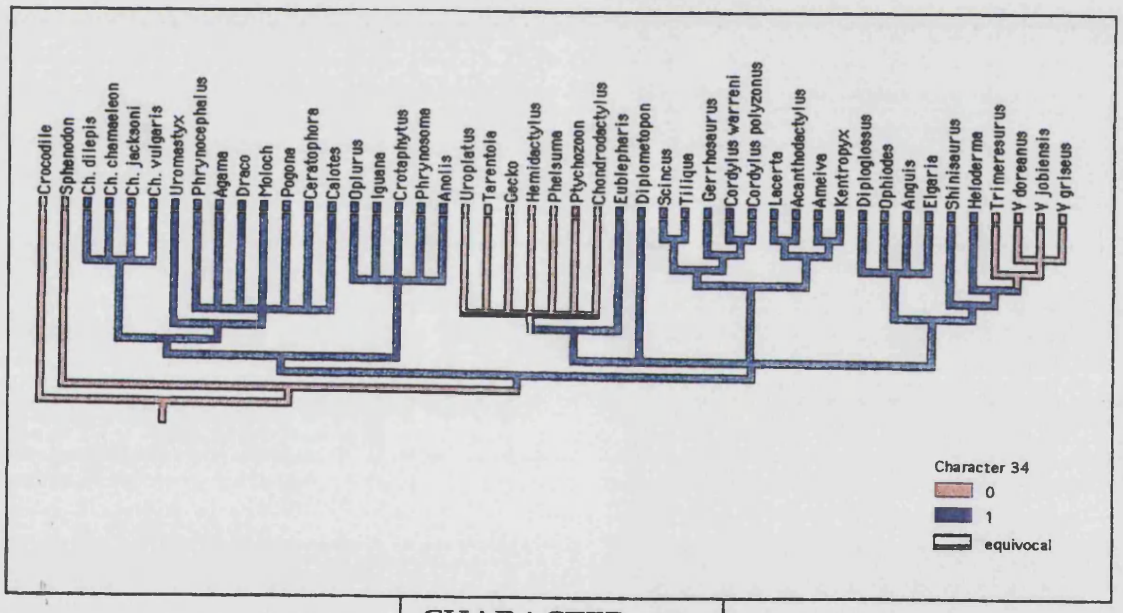


Fig. (10.7.19) *Heloderma horridum*, left ventral view of the cervical vertebrae showing the origin of longus colli (Lci) from C8 centrum. Scale bar = 1 mm.



CHARACTER .34.

35) Origin of longus colli

(0) Midline and lateral heads
(*Sphenodon*, iguanids, agamids, scincids, cordylids)
(1) Midline origin only
(*Caiman*, chamaeleons, *Trimeresurus*, *Diplometopon*, gekkotans, lacertids, teiids, anguimorphs)

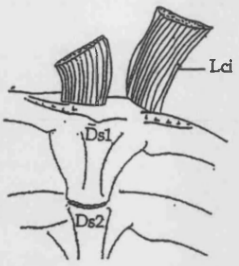
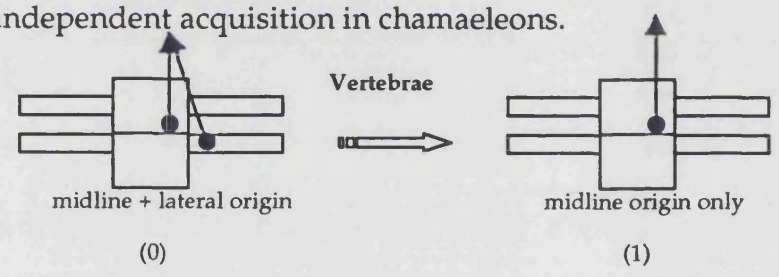
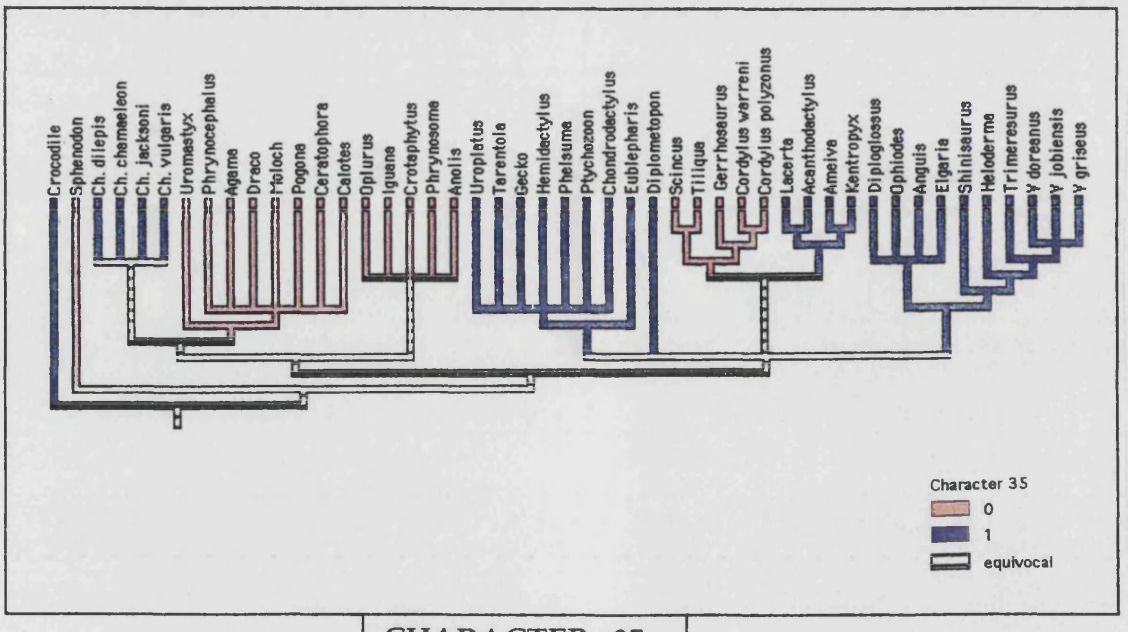


Fig. (10.7.20) *Ameiva ameiva*, ventral view of the dorsal vertebrae showing the origin of the longus colli (Lci) from the central midline. Scale bar = 1 mm.

The muscle originates by two heads from the vertebrae (midline and lateral) (0) or by one head (centra or intercentra) (1). The presence of 2 heads in *Sphenodon* and most iguanians suggests this is a primitive character in which case the derived state developed by the loss of the lateral origin. The character appears to have a clear family distribution, e.g. scincids and cordylids show the primitive state. The most likely explanation is that the derived state occurred in scleroglossans (e.g., teiids – Fig., 10.7.20), with reversal in scincoids and independent acquisition in chamaeleons.





CHARACTER .35.

36) Division of longus colli

(0) Divided into three parts
(*Sphenodon, Scincus, Shinisaurus*)
(1) Divided into two parts
(*Caiman*, agamids, iguanids)
(2) Single bundle
(chamaeleons, gekkotans, *Trimeresurus, Diplometopon, Tiliqua,* cordylids, lacertids, teiids, varanids, *Heloderma*, anguids)

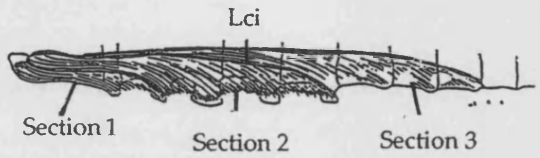


Fig. (10.7.21) Sketch drawing of *Shinisaurus crocodilurus showing* left ventrolateral view of the cervical vertebrae where the longus colli (Lci) extends in 3 sections.

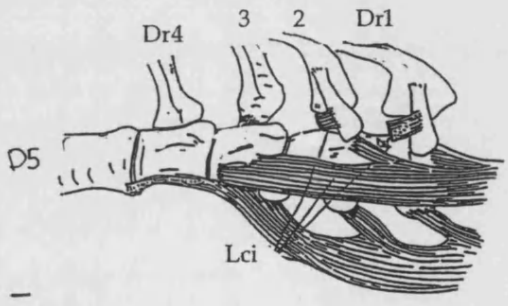
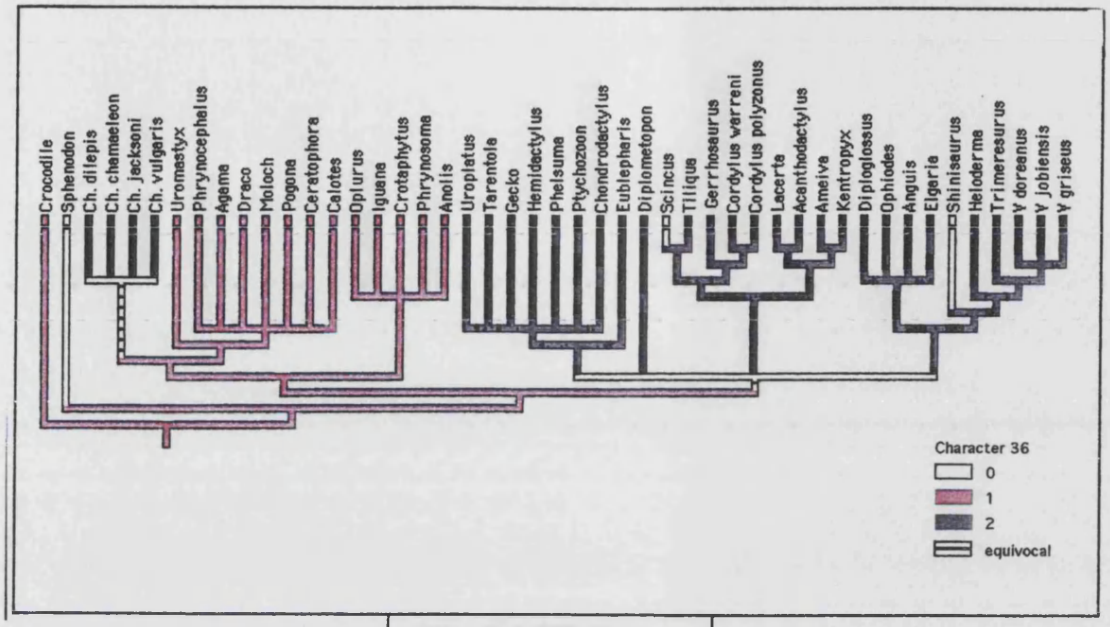


Fig. (10.7.22) *Caiman crocodilus,* right ventrolateral view of the dorsal vertebrae showing the origin of longus colli (Lci) as two bundles from the posterior cervical vertebrae. Scale bar = 1 mm.

The muscle extends along the vertebrae as (1-3) bundles. The polarity is problematic since *Sphenodon* has 3 bundles, while *Caiman* and most iguanians have 2 (Fig., 10.7.22). One bundle, at least, seems to be a derived condition present in most scleroglossans (except *Scincus, Shinisaurus*) and chamaeleons. If character state (1) is plesiomorphic, we must assume independent acquisition of an extra head (0) occurred in *Sphenodon, Scincus* and *Shinisaurus* (Fig., 10.7.21). State (2) may be a scleroglossan character.



CHARACTER .36.

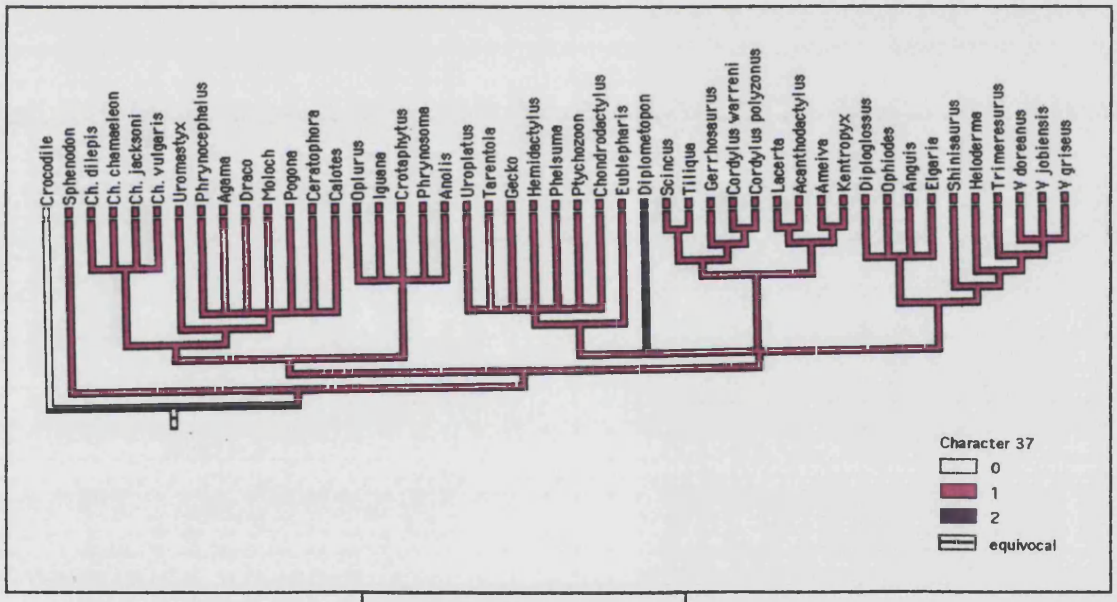
37) Insertion of longus colli

(0) Insertion as two bundles – one on basioccipital and one on oto-occipital (*Caiman*)
(1) Inserts as a single bundle on basioccipital (most groups)
(2) Inserts as a single bundle spanning the oto-occipital/lateral basioccipital lateral suture (*Diplometopon*)

The muscle divides to insert on the basioccipital and paroccipital process in *Caiman* (Fig., 10.7.23), but in most groups including *Sphenodon*, it inserts only on the basioccipital, as one bundle. This is probably the primitive state. The character may split Archosauria (*Caiman*) from Lepidosauria. In birds, the muscle does not appear to attach to the skull at all (Berge and Zweers, 1993), while in mammals part of the muscle attaches to the skull as longus capitis (basioccipital: Penning, 1968). In humans,

Fig. (10.7.23) *Caiman crocodilus*, ventral view of the craniocervical region showing the two bundles of longus colli (Lcic & Lcil) which insert on the skull (basioccipital & oto-occipital). Scale bar = 1 mm.

the muscle inserts on the basilar part of the occipital bone (Clemente, 1985; Filan, 1990; Agur et al., 1991; Warfel, 1993; Netter, 1998). So the insertion of longus colli on the skull as one bundle seems to be the widespread feature (plesiomorphy), and the double insertion of the muscle on the skull in *Caiman* is derived (more dissection is needed of crocodiles, turtles and primitive birds). In *Diplometopon* the muscle inserts as a single broad layer on both the oto-occipital and basioccipital without dividing into two bundles. This modification could be an adaptation to burrowing, but a wider survey of amphisbaenians would be needed to verify it.



CHARACTER .37.

38) Longus colli – presence or absence of the tendon of insertion.

(0) Present
(*Sphenodon*, most scincomorphs [except *Gerrhosaurus*], varanids, *Heloderma*, *Elgaria*, iguanians [except *Iguana*])
(1) Absent
(*Caiman*, *Trimeresurus*, *Diplometopon*, gekkotans, *Gerrhosaurus*, *Shinisaurus*, *Diploglossus*, *Ophiodes*, *Anguis*, *Iguana*)

The tendon of insertion, if present, can be long or short, wide or narrow (Fig., 10.7.24). The polarity is problematic. In birds there is no attachment to the skull (Berge and Zweers, 1993), while in mammals the attachment is fleshy (Penning, 1968). In humans, the muscle also lacks a tendon of insertion (Clemente, 1985; Filan, 1990; Agur et al., 1991; Warfel, 1993; Netter, 1998). State (0) is obviously basal to lepidosaurs with independent loss (1) in gekkotans, a subset of anguids, *Iguana*, *Gerrhosaurus*, *Shinisaurus*, and the snake and amphisbaenian dissected.

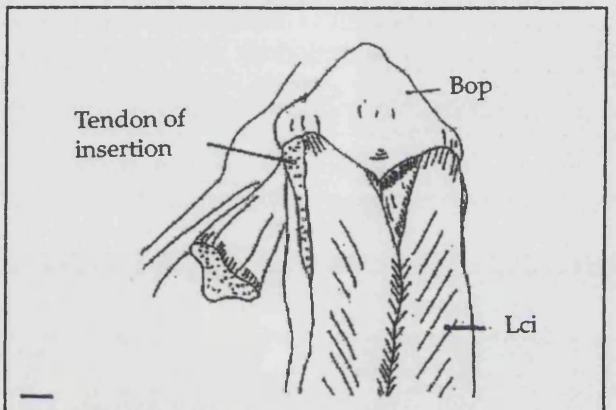
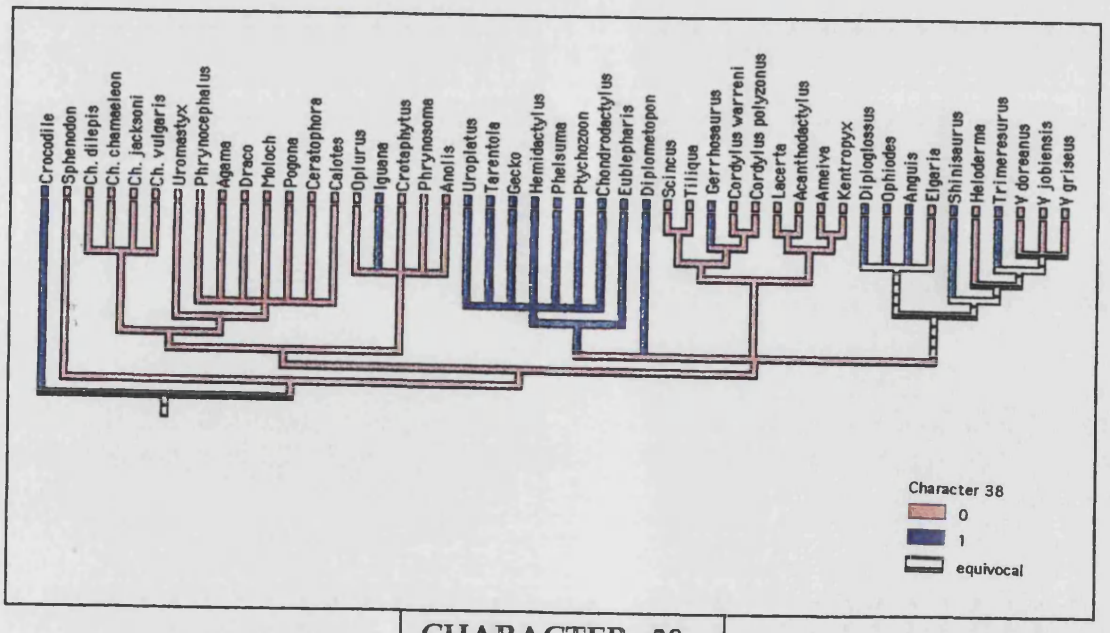


Fig. (10.7.24) *Sphenodon*, ventral view of the craniocervical region showing the tendon of insertion of the longus colli (Lci). Scale bar = 1 mm.

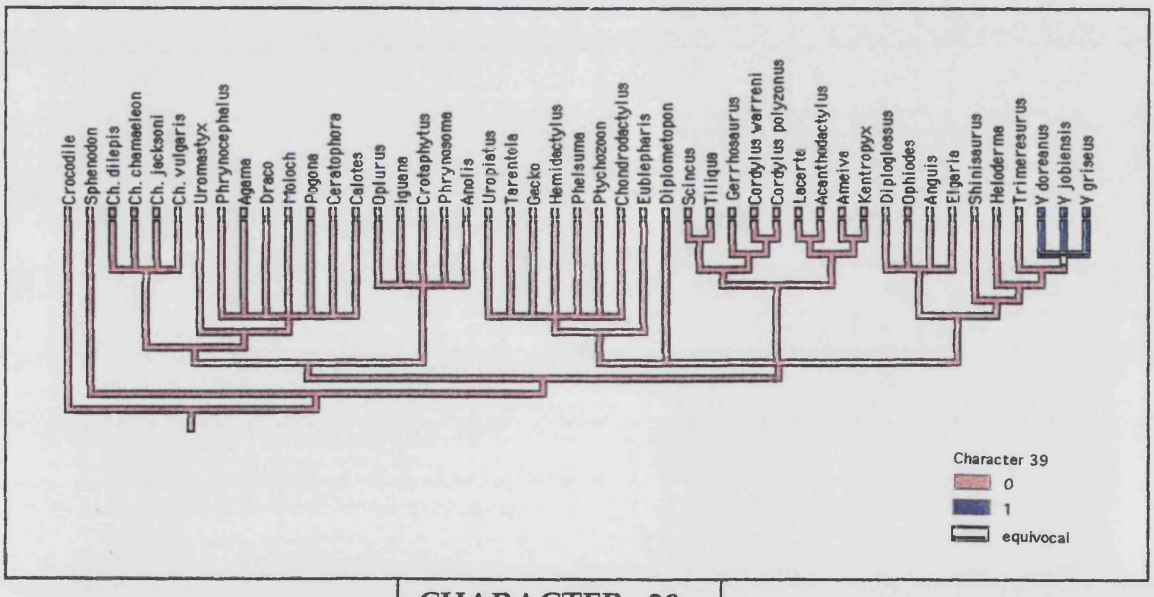


CHARACTER .38.

39) Longus colli tendon of insertion

(0) Straight
(most groups)
(1) Curved around long basal tubera
(varanids)

This character separates varanids (1) from the other groups dissected (0). In varanids and *Trimeresurus* the longus colli extends along the vertebral midline, but in the latter the muscle inserts centrally on the basioccipital. In varanids the muscle runs centrally along the basioccipital, but then becomes tendinous and curves laterally to end on the basal tubera. The central position of the longus colli on the basioccipital in varanids and *Trimeresurus* may be a shared character, but further dissections of more basal snakes are needed to verify this.



CHARACTER .39.

40) Presence or absence of longus cervicus

(0) Present
(*Sphenodon*, iguanids, agamids, gekkotans, scincomorphs, *Ophiodes, Diploglossus*)
(1) Reduced
(varanids, *Shinisaurus, Heloderma, Elgaria, Diplometopon*)
(2) Absent
(*Caiman*, chamaeleons, *Trimeresurus*)

Note: The muscle was not investigated in *Anguis fragilis.*

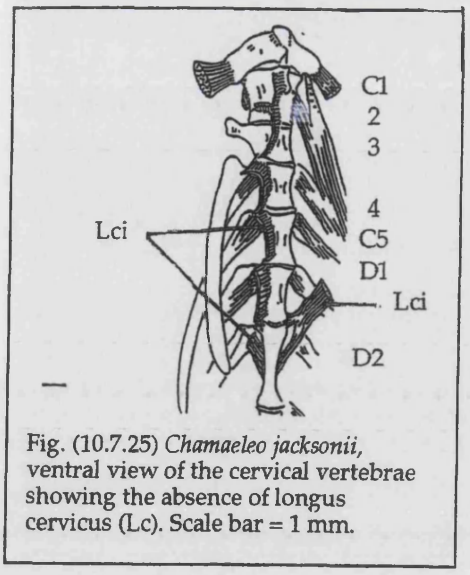
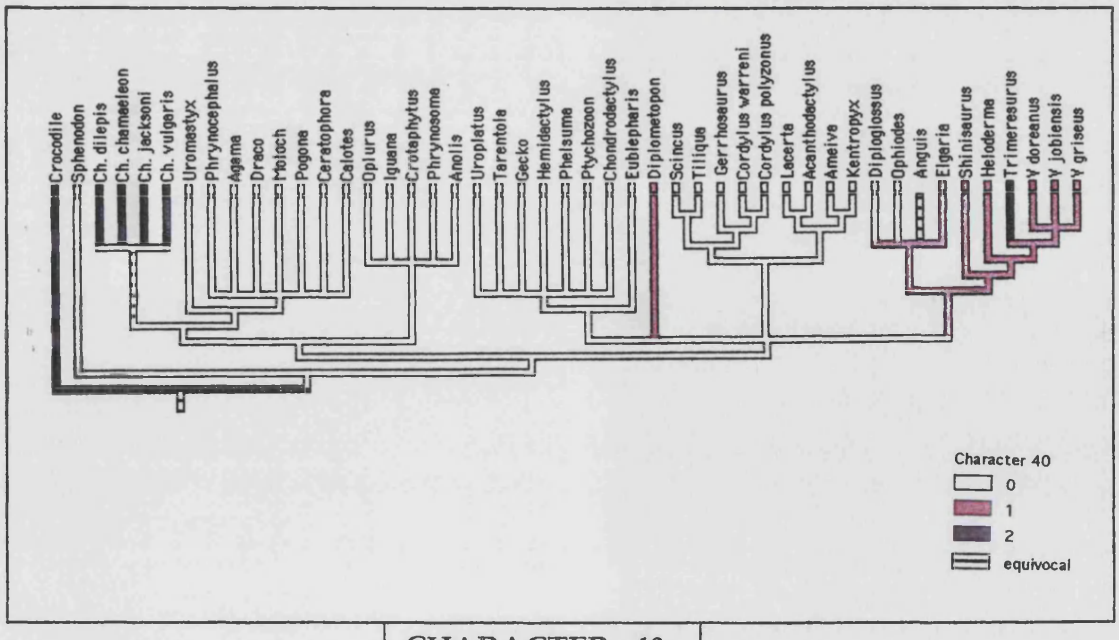


Fig. (10.7.25) *Chamaeleo jacksonii,* ventral view of the cervical vertebrae showing the absence of longus cervicus (Lc). Scale bar = 1 mm.

The muscle is present in all taxa examined, except *Caiman,* chamaeleons and *Trimeresurus*. However, in *Diplometopon* and most anguimorphs (except *Ophiodes* and *Diploglossus*) the muscle is reduced to a few long (varanids and *Diplometopon*) or short (*Shinisaurus* and *Elgaria*) tendons. The reduction of the muscle may therefore be part of an evolutionary transition from presence to complete absence of longus cervicus. In mammals the muscle is present (Filan, 1990; Clemente, 1985; Agur et al., 1991; Warfel, 1993; Netter, 1998), so character state (0) may be basal for lepidosaurs with state (2) derived independently in chamaeleons (Fig., 10.7.25) and *Trimeresurus* (more dissection is needed). Character (1) may be a synapomorphy of a subset of anguimorphs.



CHARACTER .40.

41) Origin of longus cervicus

(0) Dorsal vertebrae
(*Sphenodon, Crotaphytus, Phrynosoma, Moloch, Draco, Agama, Pogona, Calotes, Uroplatus*, varanids)
(1) Cervical vertebrae +/- D1
(*Oplurus, Anolis, Iguana, Uromastyx, Ceratophora, Phrynocephalus*, eublepharids, most gekkonids (except *Uroplatus*), scincomorphs, *Shinisaurus*, anguids, *Heloderma*)

Polarity is problematic. Character state (0) occurs in Acrodonta above *Uromastyx*, and has also present in varanids. Character state (1) is probably the basal condition of squamates (e.g. iguanids – Fig., 10.7.26). In some dissected gekkonids (*Hemidactylus, Tarentola, Chondrodactylus*) the muscle originates from the 9th intercentrum (between C8 and D1) a more derived state than that of *Phelsuma, Gekko, Ptychozoon* and *Eublepharis* (C7-8). More dissection of gekkotans is needed, including pygopodids.

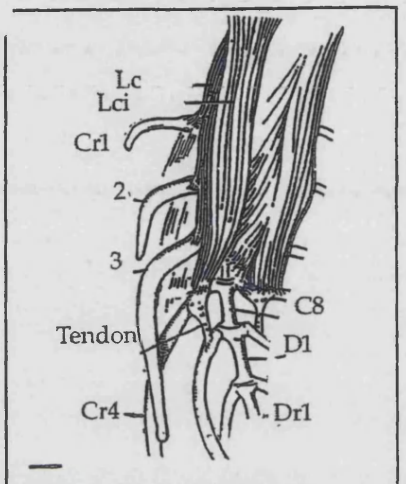
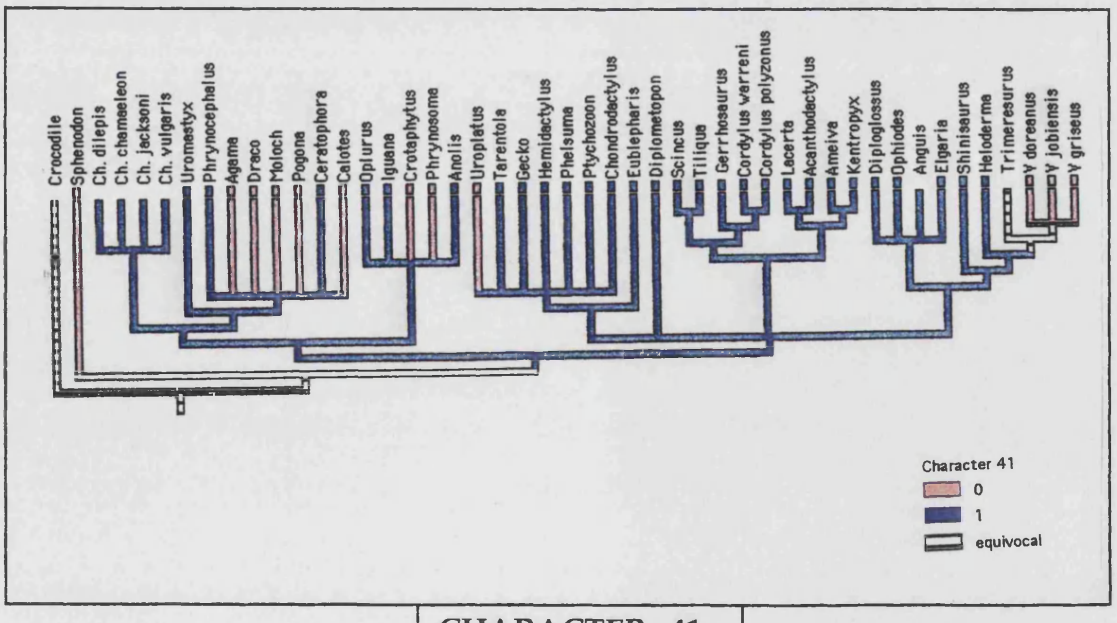


Fig. (10.7.26) *Anolis richardii*, ventral view of the cervical region showing the origin of longus cervicus (Lc) from cervical vertebrae (8 centrum & rib). Scale bar = 1 mm.

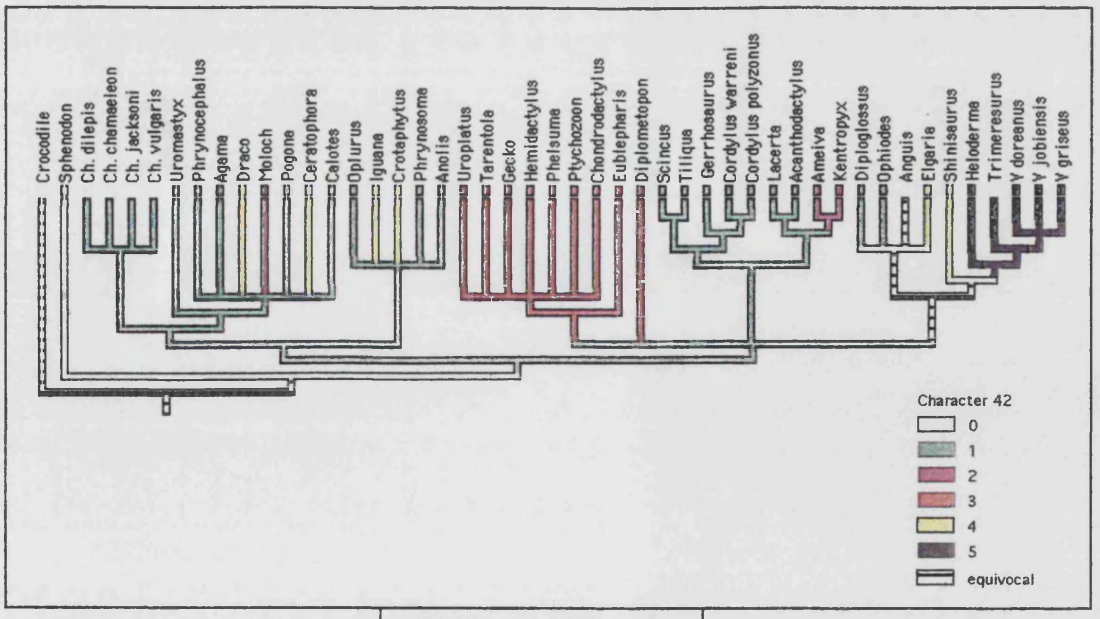


CHARACTER .41.

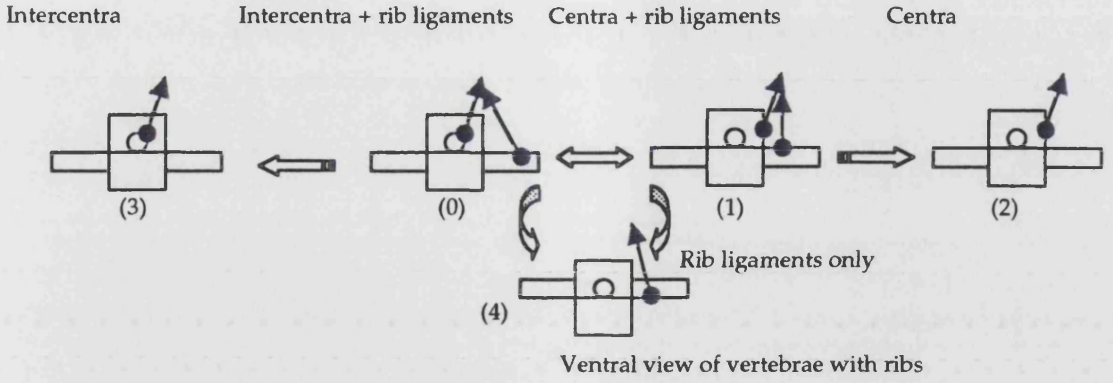
42) Longus cervicus begins from

(0) Intercentra and rib ligaments
(*Sphenodon*)
(1) Centra and rib ligaments
(*Oplurus, Anolis, Phrynosoma, Uromastyx, Calotes, Phrynocephalus, Pogona*, scincids, lacertids, cordylids, *Diploglossus, Ophiodes*)
(2) Centra only
(*Eublepharis, Moloch*, teiids)
(3) Intercentra (hypapophysis) only
(gekkonids, *Diplometopon*)
(4) Rib ligaments only
(*Draco, Ceratophora, Crotaphytus, Iguana, Elgaria, Shinisaurus*)
(5) Rib and rib ligaments
(*Heloderma*, varanids)

The character shows considerable variation, but character state (1) appears to be the basal squamate condition, with random variation within iguanians. State (2) may characterise teiids (more dissection is needed), while state (3) appears to be a gekkonid synapomorphy shared by *Diplometopon*, but is not shared by eublepharids. State (4) occurs in diverse several taxa. State (5) characterizes Varanoidae (varanids and helodermatids). A dissection of *Lanthanotus* may support this observation.



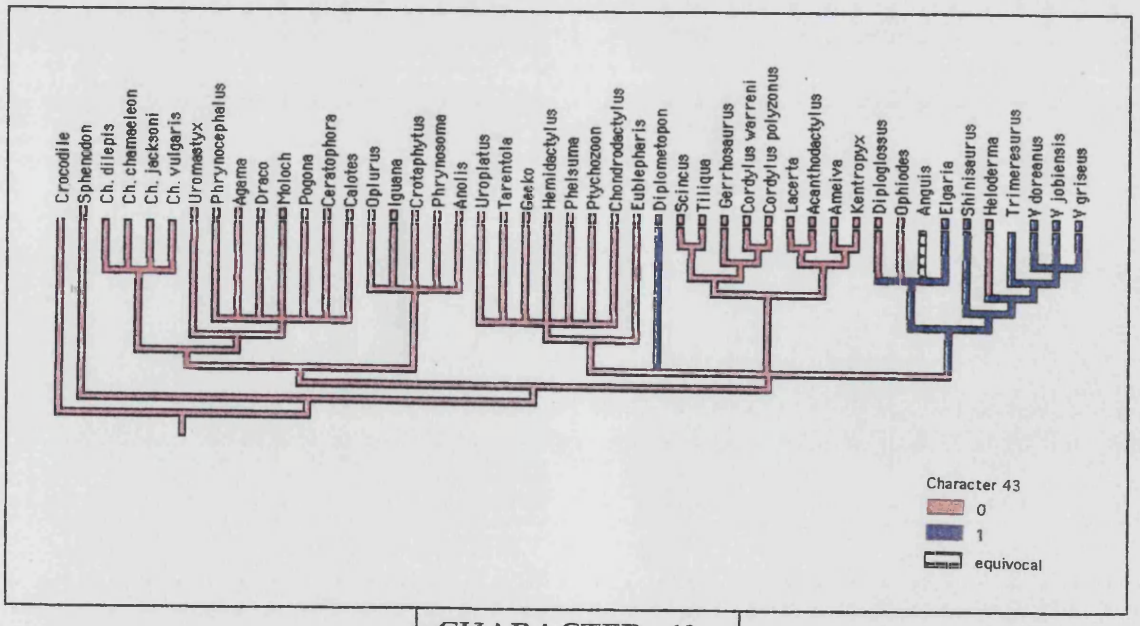
CHARACTER .42.



43) Longus cervicus muscular or tendinous

(0) Muscular
(*Sphenodon*, agamids, iguanids, gekkotans, scincomorphs, *Diploglossus*, *Ophiodes*, *Heloderma*)
(1) Tendinous
(varanids, *Diplometopon*, *Shinisaurus*, *Elgaria*)

The muscle is fleshly in most taxa (0) but the reduction of longus cervicus to a tendinous bundle (1) is found in *Diplometopon* and some dissected anguimorphs (except *Ophiodes*, *Diploglossus*, *Heloderma*). More dissections of anguimorphs and amphisbaenians are needed.



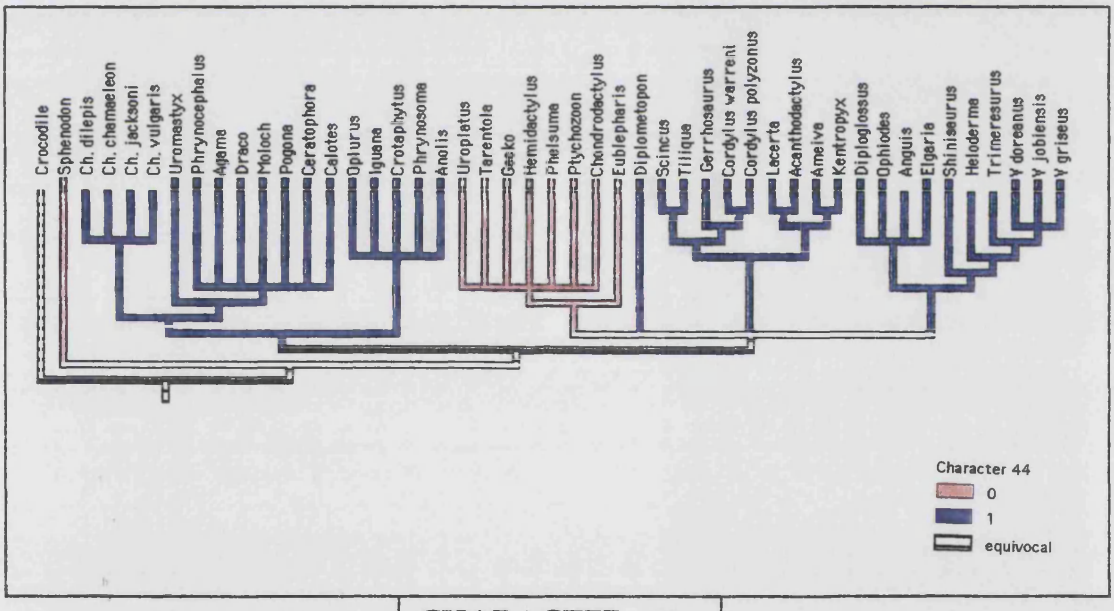
CHARACTER .43.

44) Longus cervicus – number of heads

(0) Two heads – medialis and lateralis
(*Sphenodon*, gekkotans)
(1) Single head
(iguanids, agamids, scincomorphs, anguimorphs, *Diplometopon*)

In *Sphenodon* and gekkotans the longus cervicus inserts on the second and third intercentra (lateral crests) by separate heads (0). In all other groups examined, the muscle forms a narrow bundle with a single head of insertion (1). The condition in gekkotans is presumably secondary and perhaps linked to paedomorphosis.

Polarity is problematic, because the muscle was absent in *Caiman*, but (1) appears to be the basal squamate condition with (0) characterising gekkotans.



CHARACTER .44.

45) Length of longus cervicus in relation to longus colli

(0) Cervicus longer than colli
(*Sphenodon*, varanids)
(1) Cervicus equal in length to colli
(*Iguana, Crotaphytus, Moloch, Calotes, Phrynocephalus, Agama, Pogona*, gekkotans, *Heloderma*)

(2) Cervicus shorter than colli
(*Oplurus, Anolis, Phrynosoma, Uromastyx, Draco, Ceratophora,* scincomorphs, most anguimorphs, *Diplometopon*)

Longus cervicus is longer than longus colli in *Sphenodon* (0) (Fig. 10.7.27), but equal or shorter in a majority of squamates (1 and 2). The two muscles are equal in gekkotans and shorter in all scincomorphs, but the condition varies in iguanians and anguimorphs (Fig. 10.7.28). In *Diplometopon*, the longus cervicus is reduced and is shorter than longus colli (21 vertebra), while varanids converge with *Sphenodon* and have a longer longus cervicus – again perhaps as a function of the long neck.

Polarity is problematic but state (0) characterised varanids, while state (1) appears to be a synapomorphy of gekkotans, also present in some iguanids without a clear pattern. Character state (2) seems to be that of basal squamates.

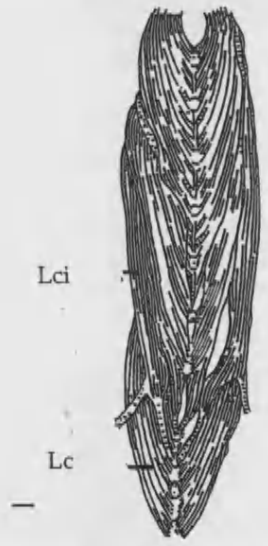


Fig. (10.7.27) *Sphenodon*, ventral view of the craniocervical region showing the longus cervicus (Lc) > longus colli (Lci). Scale bar = 1 mm.

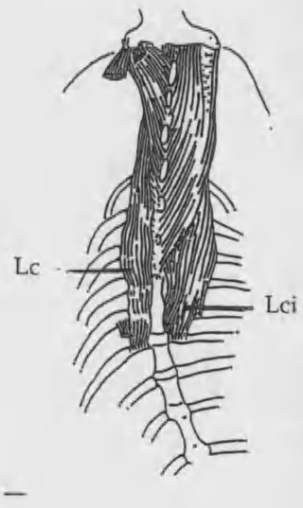


Fig. (10.7.28) *Crotaphytus collaris*, ventral view of the craniocervical region showing longus cervicus (Lc) = longus colli (Lci). Scale bar = 1 mm.

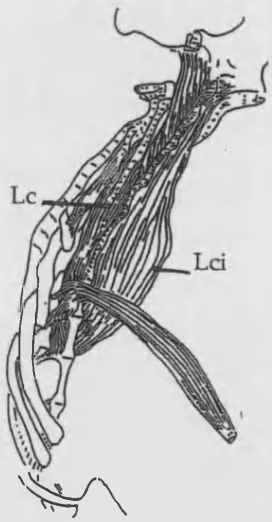
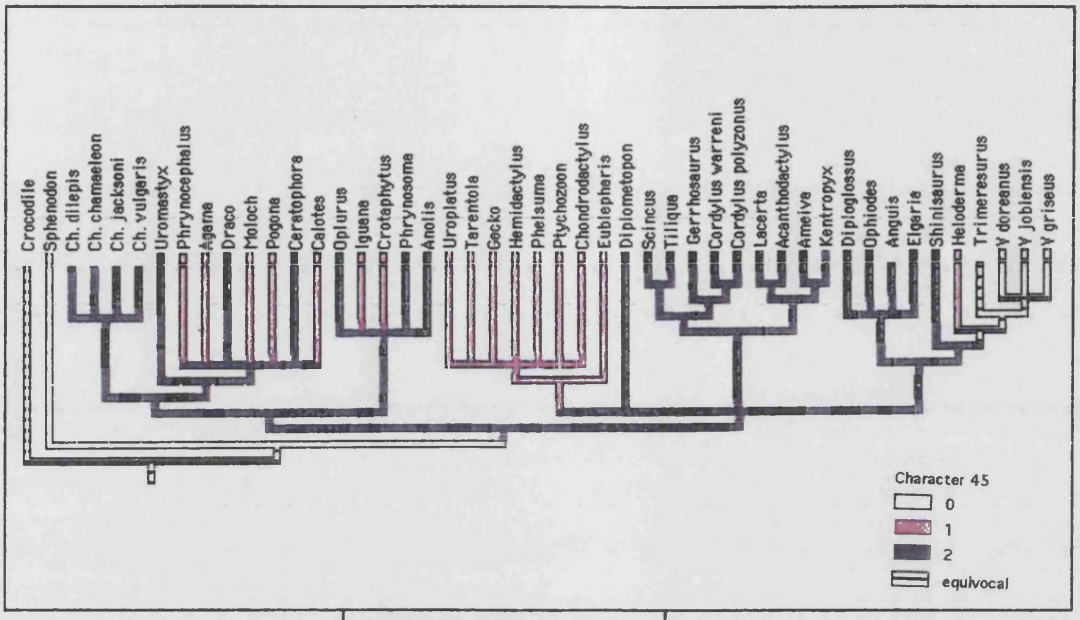


Fig. (10.7.29) *Oplurus cyclurus*, ventral view of the craniocervical region showing longus cervicus (Lc) < longus colli (Lci). Scale bar = 1 mm.



CHARACTER .45.

The precise length of the longus colli and cervicus is variable within and between species, but the variation is consistent within states.

46) First intercentrum to skull muscle, insertion

(0) Basioccipital
(most groups)
(1) Basioccipital and oto-occipital
(scincomorphs, iguanians)

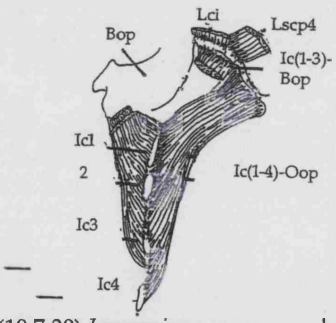
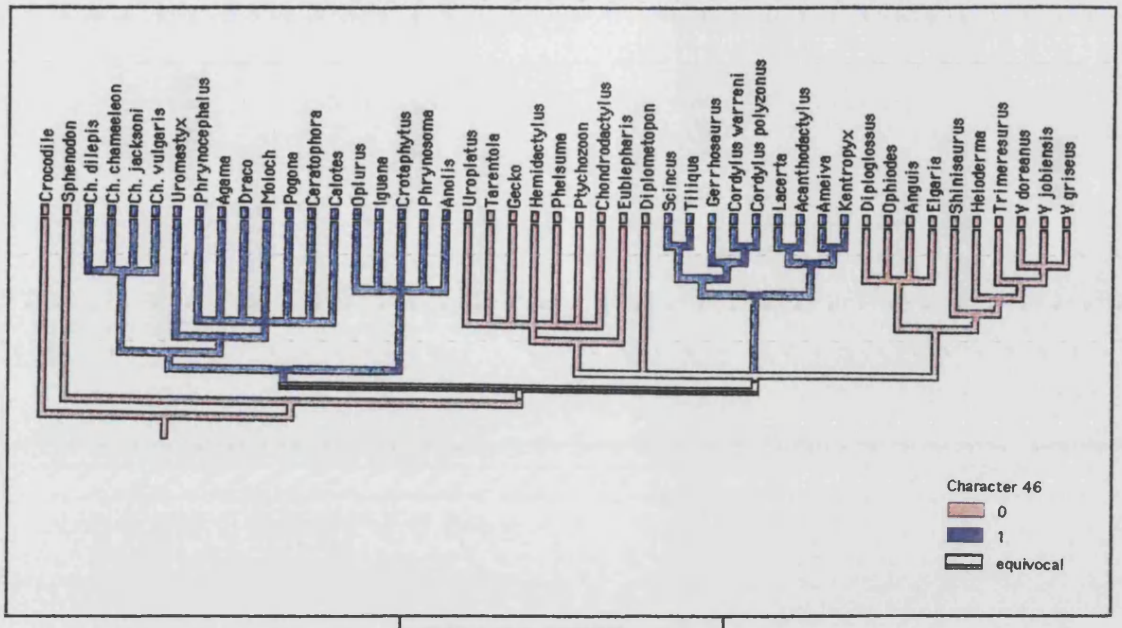


Fig. (10.7.30) *Iguana iguana*, ventral view of the craniocervical region showing the insertion of the 1st intercentral muscle to basioccipital & oto-occipital (Ic1-Bop&Oop). Scale bar = 1 mm.

Character state (0) is probably plesiomorphic, overall, but the basal squamate condition is equivocal. It could be (0) with (1) as a derived condition in Iguania and scincomorphs (Fig., 10.7.30). Alternatively, (0) could be the basal squamate state, with reversal occurring in gekkotans and anguimorphs (together or separately).



CHARACTER .46.

47) The superficial branch of the first intercentrum to skull muscle inserts on the basioccipital.

(0) Completely deep to longus colli
(*Sphenodon*, varanids, *Heloderma, Shinisaurus, Ophiodes, Anguis, Trimeresurus*)
(1) Partially deep to longus colli
(*Caiman*, iguanids [except *Iguana*], chamaeleons, agamids [except *Uromastyx* juveniles], gekkotans, scincomorphs, *Elgaria, Diploglossus, Diplometopon*)

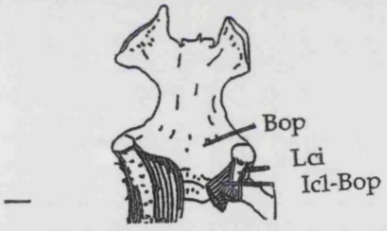
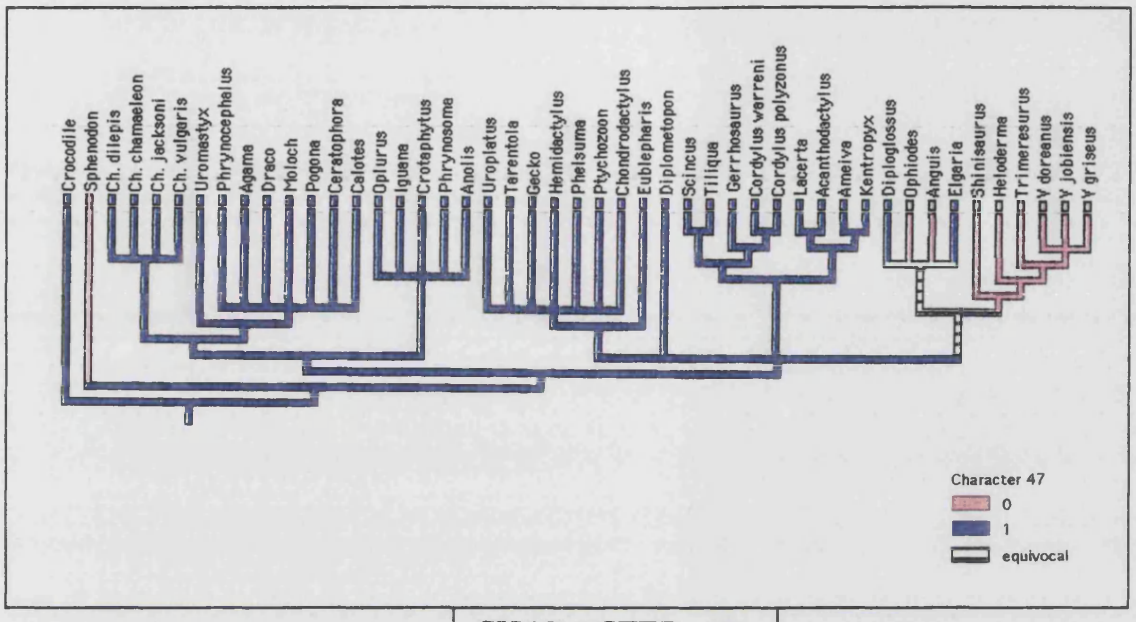


Fig. (10.7.31) *Heloderma horridum*, ventral view of the skull showing the insertion of 1st intercentral muscle slip (Ic1-Bop) completely under longus colli (Lci). Scale bar = 1 mm.

Most anguimorphs examined (except *Diploglossus* and *Elgaria*) and *Trimeresurus* share condition (0) with *Sphenodon* where the muscle inserts completely under longus colli. Most iguanians share character (1) where the muscle inserts partially under longus colli and centrally, as in scincomorphs and *Diplometopon*, but the juvenile *Uromastyx* showed a diverging insertion of the first intercentral muscle on the basioccipital ([0] or [1] state). The muscle in all gekkotans is only partly covered

by longus colli (1). Character state (1) may be plesiomorphic for Squamata with state (0) characterizing a subset of anguimorphs (e.g. *Heloderma,* Fig., 10.7.31).



CHARACTER .47.

48) As seen in ventral view, posterior intercentral muscle slips insert on the skull under longus colli and

(0) Superficial and lateral to the first intercentral muscle
(*Sphenodon, Heloderma,* Iguania, scincomorphs, *Trimeresurus*)
(1) Deep to the first intercentral muscle
(gekkotans, *Shinisaurus,* anguids)
(2) On the same level as the first intercentral muscle slip
(varanids, *Diplometopon*)

In *Sphenodon,* the slips attach superficial to those of the first intercentral muscle, and all iguanians and scincomorphs, as well as *Heloderma* and *Trimeresurus* share this (presumably primitive) state (Fig., 10.7.33).

Character state (1) links gekkotans and some anguimorphs (*Shinisaurus* and anguids). The derived character state (2) is present in amphisbaenians (*Diplometopon*) and varanids.

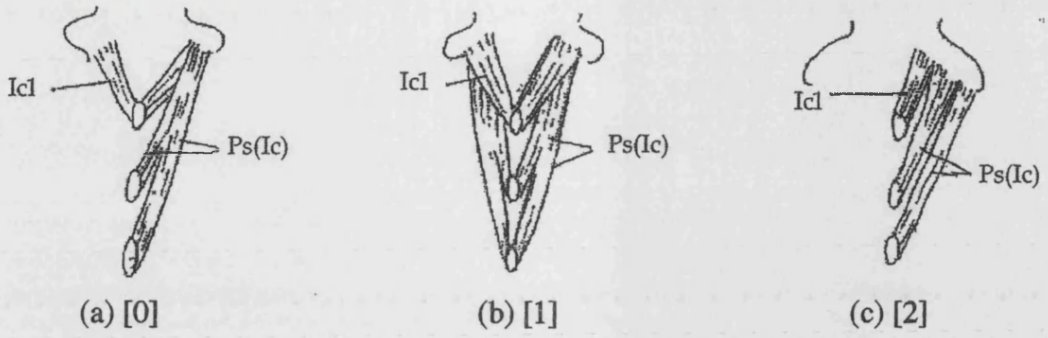


Fig. (10.7.32) Sketch drawing of position of insertion of posterior intercentral ([Ps]Ic) muscle slips in relation to 1st intercentral (Ic1) muscle slip to skull a) superficial [0]; b) deep [1]; c) same level [1].

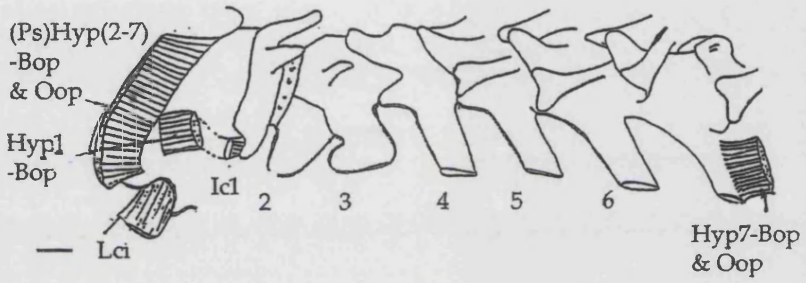
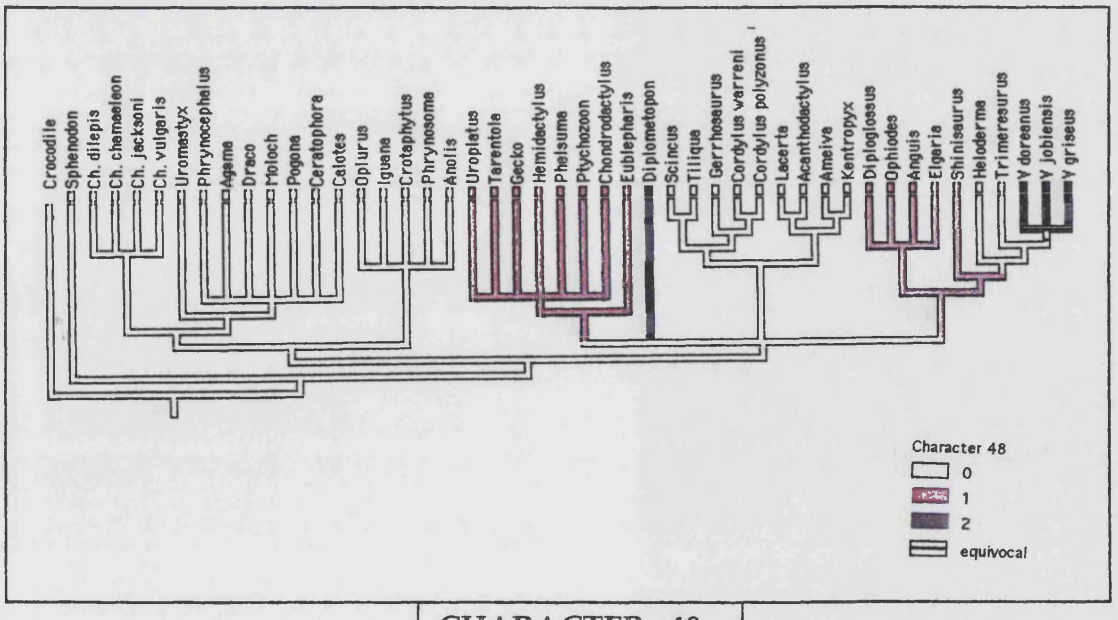


Fig. (10.7.33) *Trimeresurus wagleri*, left ventrolateral view of the anterior vertebrae showing the superficial insertion of the posterior hypapophyses muscle slips ([Ps]hyp[2-7]-Bop&Oop) to the 1st hypapophysis muscle slip (Hyp1-Bop) on the skull. Scale bar = 1 mm.

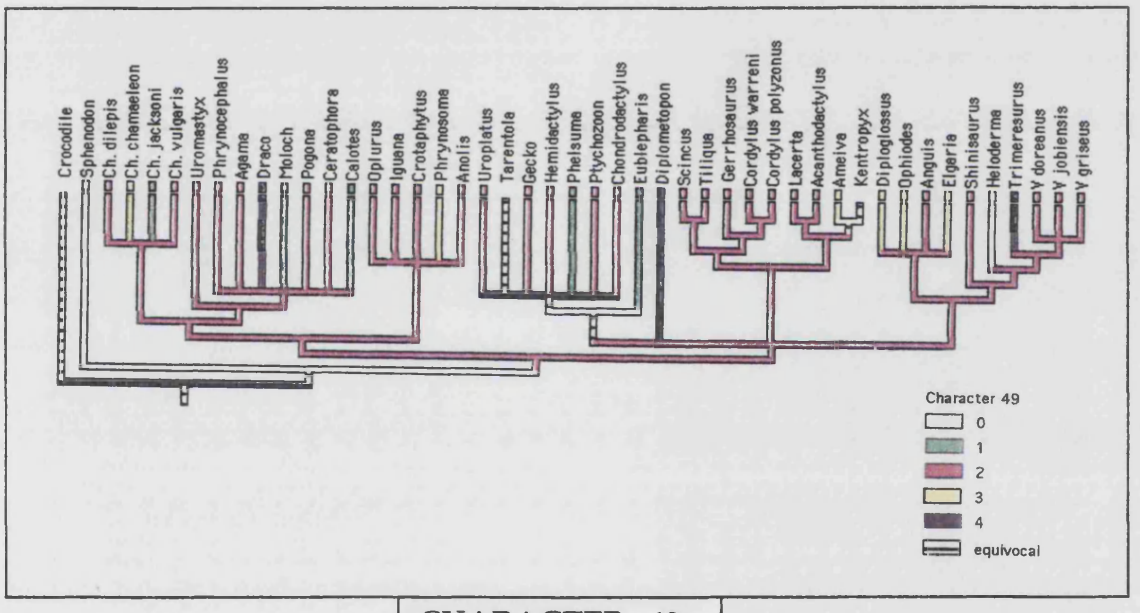


CHARACTER .48.

49) Number of postatlantal intercentrum to skull muscle slips.

(0) one – from intercentrum 3
(*Sphenodon, Heloderma*)
(1) One - from intercentrum 2
(*Phelsuma, Eublepharis, Moloch, Calotes, Chamaeleo jacksoni*)
(2) Two or three – from intercentrum 2 + 3, 2 -4
(*Hemidactylus, Gecko, Chondrodactylus, Ptychozoon, Uroplatus,* scincids, cordylids, lacertids, *Shinisaurus,* varanids, *Anguis, Uromastyx, Agama, Ceratophora, Phrynocephalus, Pogona, Chamaeleo dilepis, Crotaphytus, Iguana, Oplurus*)
(3) Four – from intercentra 2-5
(*Ameiva, Ophiodes, Phrynosoma, Chamaeleo chamaeleon*)
(4) Five or more
(*Diplometopon, Trimeresurus, Draco*)

There is considerable variation in this character, but there is some evidence that state (2) might be primitive for squamates.



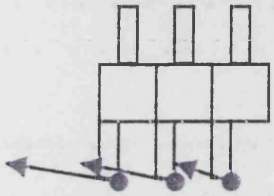
CHARACTER .49.

50) Presence or absence of muscle slips between the apices of the hypapophyses

(0) Absent
(most groups)
(1) Present
(varanids)

These slips are absent in all taxa (0) except in varanids (1) and appear to represent a special feature of this family. The hypapophyses in varanids are deep and possess lateral and median epiphyses on their apices where the muscles begin. This development may assist in the support of the long neck.

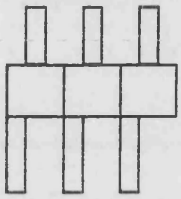
Cervical vertebrae



Apices muscle slips on the varanid hypapophyses

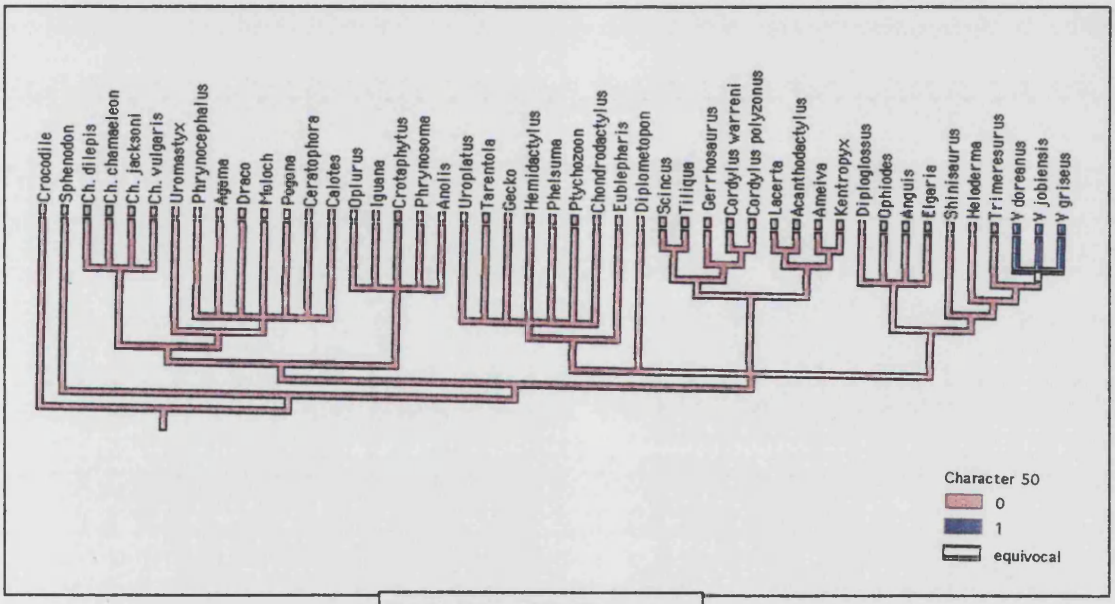
(1)

Dorsal



Ventral

(0)



CHARACTER .50.

51) Presence or absence of deep muscle slips from the intercentra to the rib ligaments

(0) Absent
(*Sphenodon*, chamaeleons, *Eublepharis*, *Heloderma*, *Shinisaurus*, anguids, *Trimeresurus*)
(1) Present
(*Caiman*, *Diplometopon*, gekkonids, scincomorphs, varanids, *Heloderma*, *Oplurus*, *Crotaphytus*, *Iguana*, *Anolis*, *Uromastyx*)

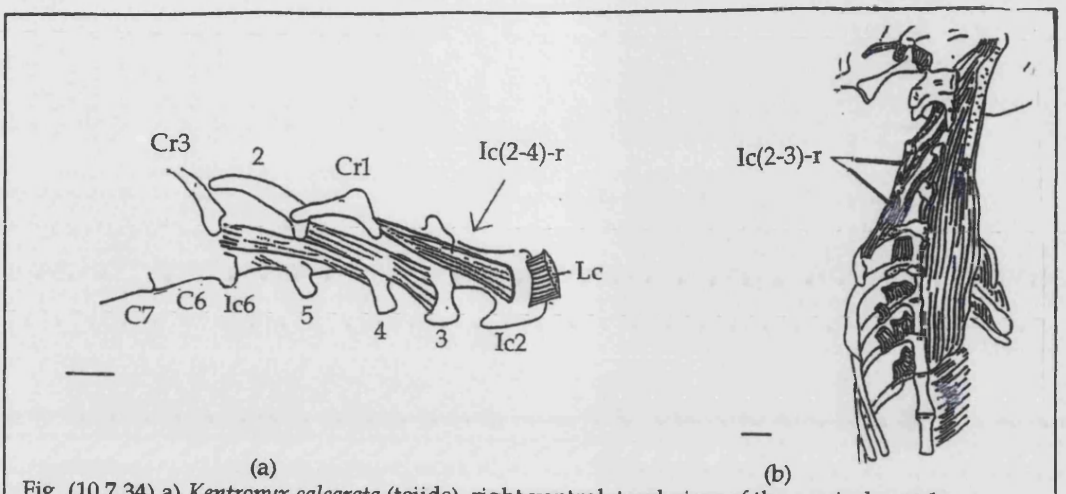
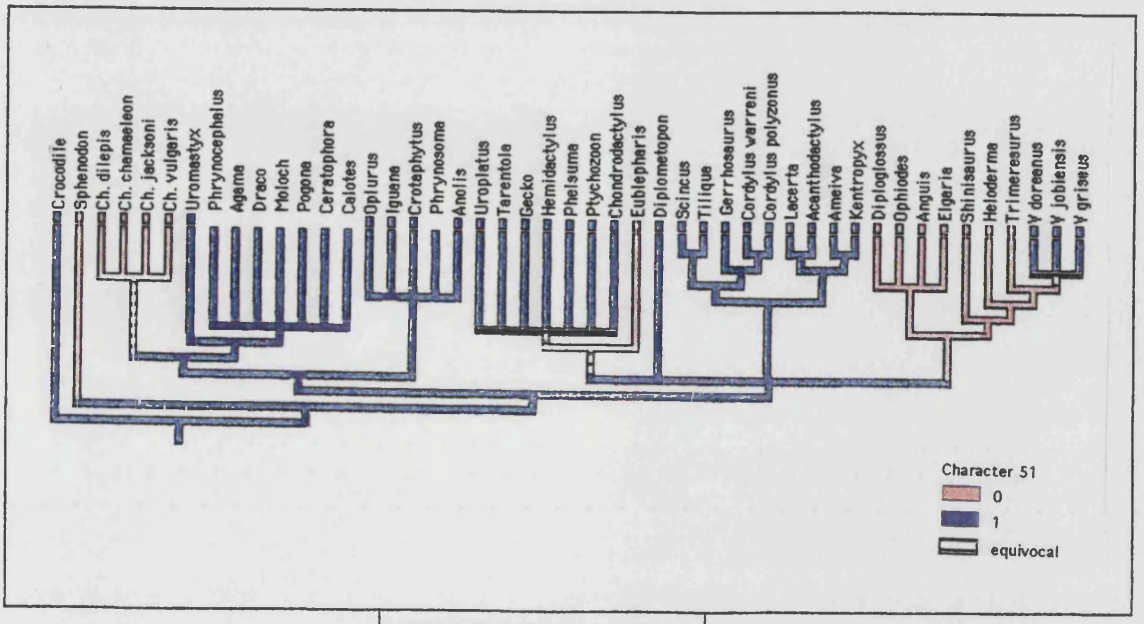


Fig. (10.7.34) a) *Kentropyx calcarata* (teiids), right ventrolateral view of the cervical vertebrae showing the extension of 2-4 intercentra to rib muscle slips (Ic[2-4]-r). b) *Oplurus cyclurus* (iguanids), ventral view of the craniocervical region showing the extension of 2-3 intercentra to rib muscle slips (Ic[2-3]-r). Scale bar = 1 mm.

These short muscle slips connect the bases of the intercentra and the rib ligaments, and extend along the cervical vertebrae in some but not all taxa. These slips could be part of iliocostalis major. The slips are absent (0) in *Sphenodon*, chamaeleons, eublepharids, many anguimorphs and *Trimeresurus*. Character state (1) appears to be plesiomorphic (Fig., 10.7.34a, b), while loss of the deep muscle slips may be a synapomorphy of chamaeleons and anguimorphs with a reversal in varanids.



CHARACTER .51.

52) Presence or absence of cervical and trunk central tendons

(0) Present
(*Sphenodon*, gekkotans, anguids, *Iguana, Oplurus, Anolis, Draco, Agama, Calotes, Pogona*)
(1) Very reduced or absent
(*Caiman, Trimeresurus, Diplometopon*, scincomorphs, varanids, *Heloderma, Shinisaurus, Phrynosoma, Crotaphytus, Uromastyx, Ceratophora, Moloch, Phrynocephalus*, chamaeleons)

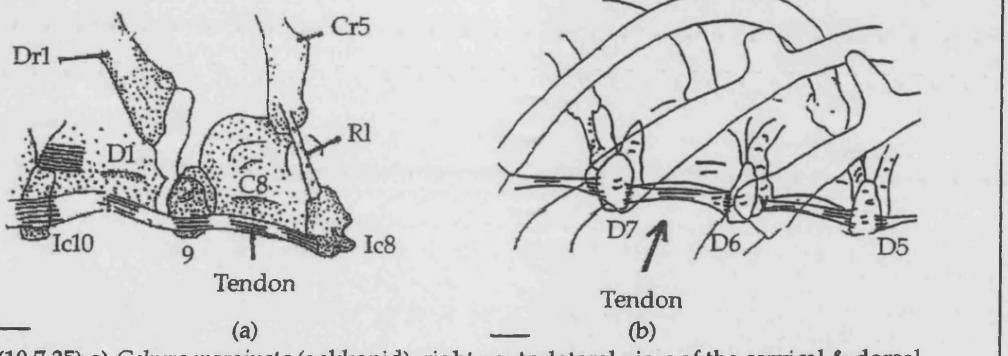
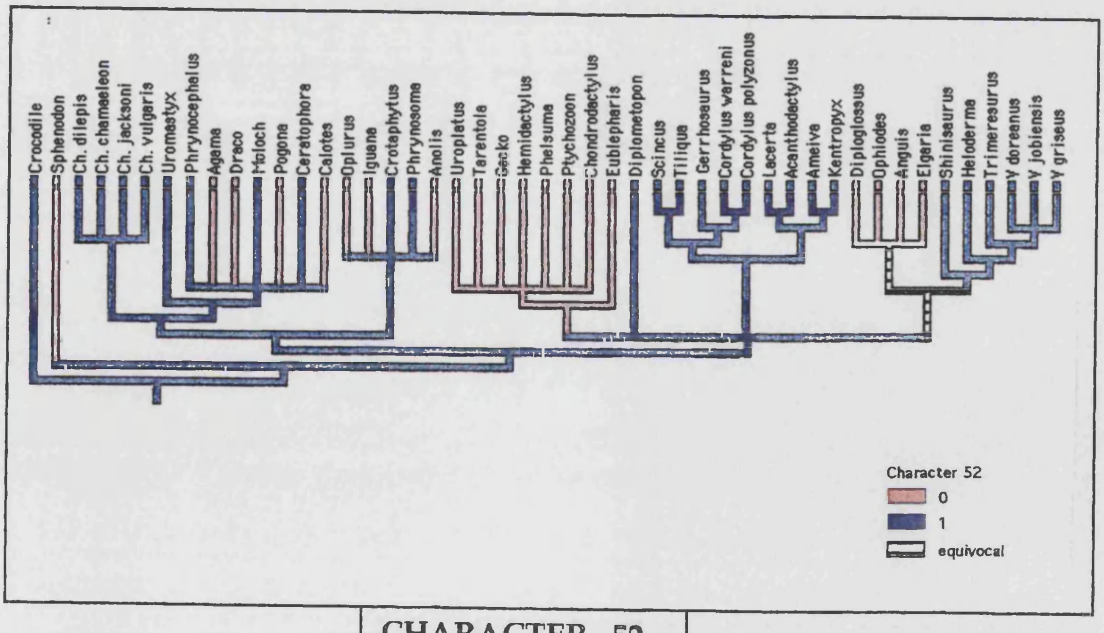


Fig. (10.7.35) a) *Gehyra marginata* (gekkonid), right ventrolateral view of the cervical & dorsal vertebrae showing the start of the ventral tendon from the last keeled intercentrum (Ic8)) & extending along the trunk. B) *Sphenodon*, right ventral view of the dorsal vertebrae showing the ventral tendon. Scale bar = 1 mm.

Character state (1) is widespread in squamates, with character state (0) as a possible synapomorphy of gekkotans (Fig., 10.7.35a), anguids and iguanids (with reversal in *Phrynosoma* and *Crotaphytus*).

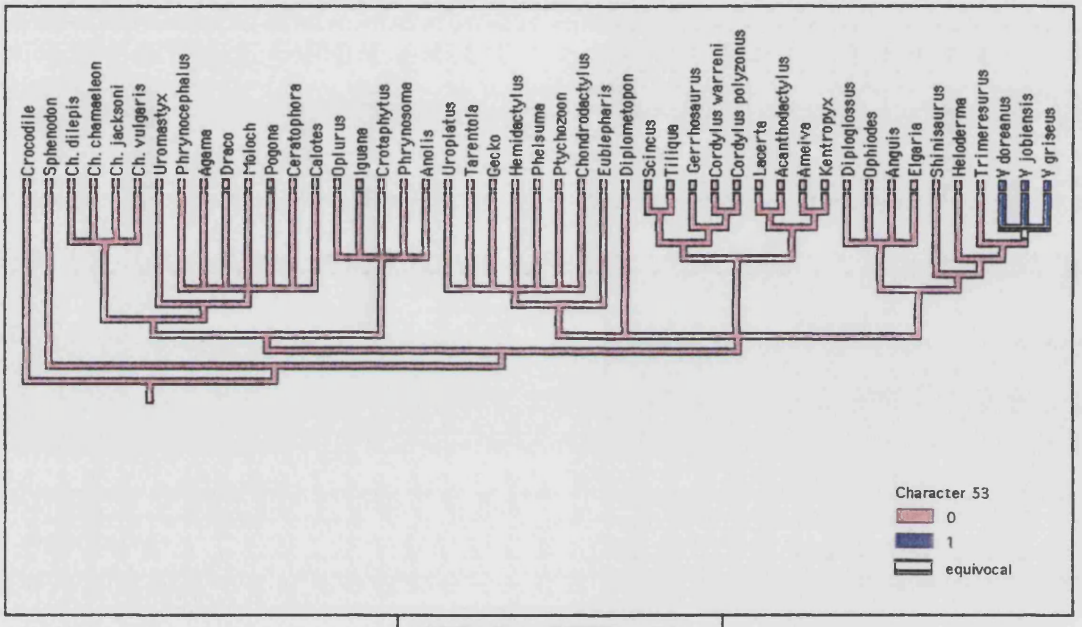


CHARACTER .52.

53) Presence or absence of muscle slips from the hypapophyses to the clavicle and scapulocoracoid.

(0) Absent
(*Sphenodon, Caiman,* most squamates)
(1) Present
(varanids)

The presence of muscle slips from the hypapophyses to the pectoral girdle (1) is an advanced character of varanids.



CHARACTER .53.

54) Presence or absence of muscle slips from the hypapophyses to the suprascapula

(0) Absent
(*Caiman, Sphenodon,* most squamates)
(1) Present
(varanids, *Diploglossus, Ophiodes*)

Character state (0) appears plesiomorphic for squamates, with (1) found in some

Anguimorphs (Fig., 10.7.36). A larger sample of anguimorphs needs to be studied.

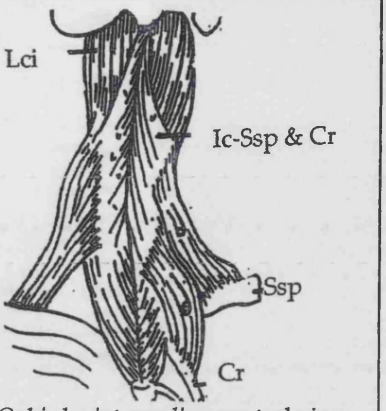
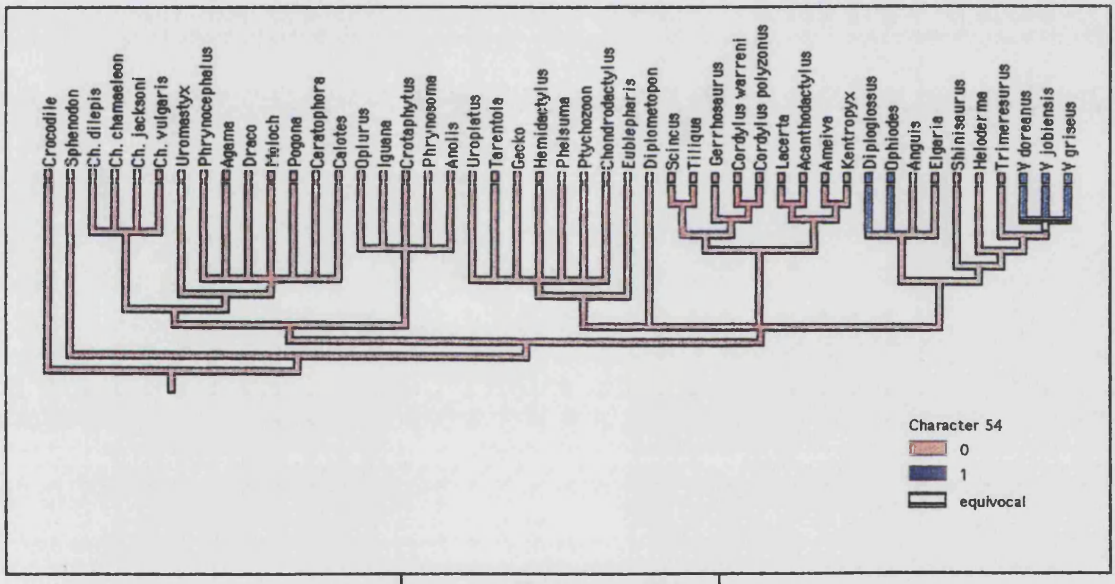


Fig. (10.7.36) *Ophiodes intermedius*, ventral view of the craniocervical region showing the intercentra to suprascapula and rib muscles slips (Ic-Spp&Cr). Scale bar = 1 mm.



CHARACTER .54.

55) Insertion of longissimus capitis 4

(0) On basal tubera only
(*Caiman, Sphenodon*, iguanids, *Uromastyx* [juvenile], scincids, cordylids, *Shinisaurus*)
(1) On basal tubera and oto-occipital
(agamids, chamaeleonids)
(2) On the oto-occipital only
(gekkotans, lacertids, teiids, anguids, *Trimeresurus*, varanids)
(3) On the lower jaw (dentary)
(*Diplometopon*)

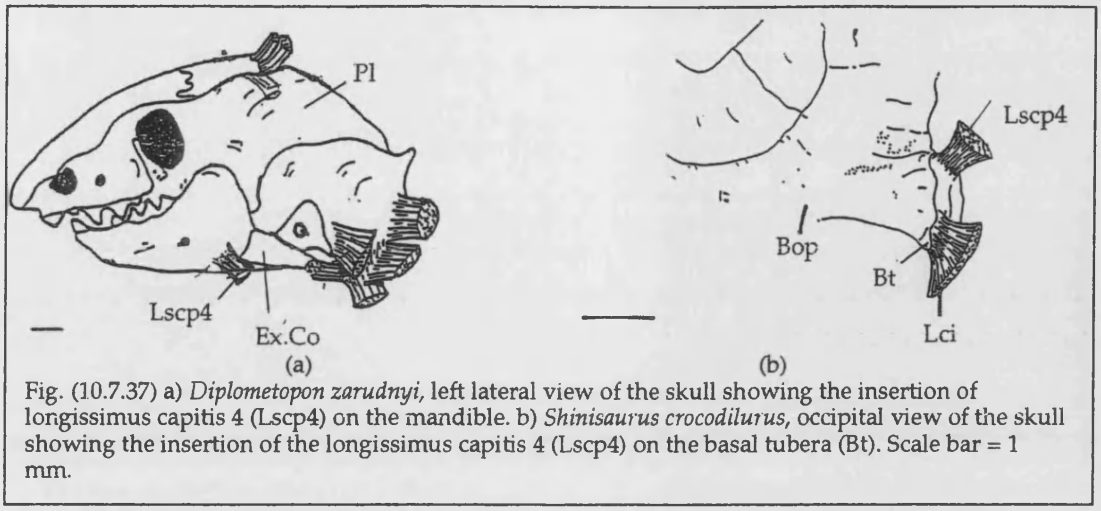
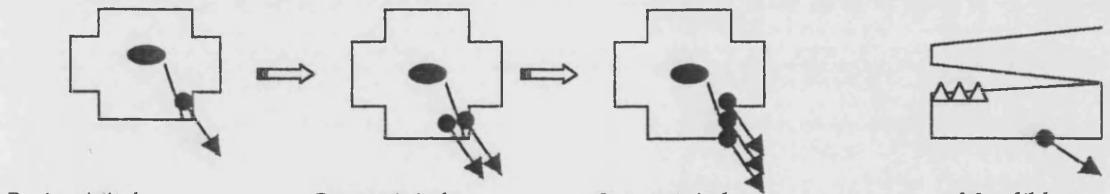


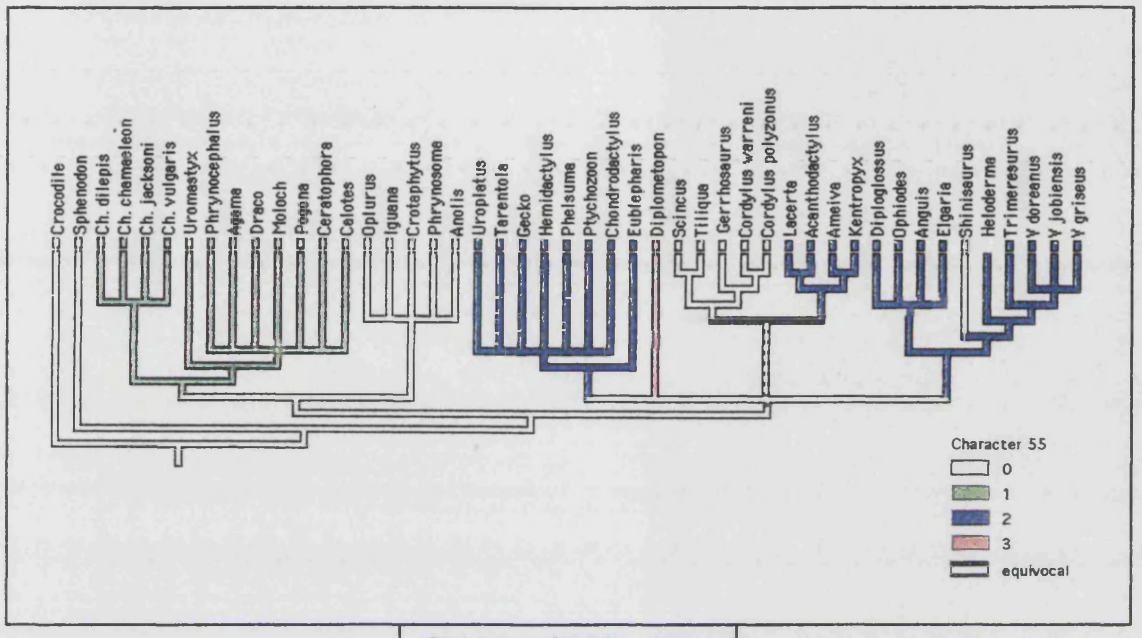
Fig. (10.7.37) a) *Diplometopon zarudnyi*, left lateral view of the skull showing the insertion of longissimus capitis 4 (Lscp4) on the mandible. b) *Shinisaurus crocodilurus*, occipital view of the skull showing the insertion of the longissimus capitis 4 (Lscp4) on the basal tubera (Bt). Scale bar = 1 mm.

The muscle insertion appears to have extended from the basioccipital (*Sphenodon*, iguanids and most scincoids [0]) onto the ventrolateral tip of the oto-occipital in agamids and chamaeleonids (Acrodonta [1]), while it shifts to insert on the oto-occipital only in gekkotans, lacertids, teiids, anguids, varanids and *Trimeresurus*. In varanoids, the muscle inserts broadly on the ventrolateral margin of the oto-occipital, while in *Diplometopon*, the muscle uniquely inserts on the mandible [3] (Fig., 10.7.37a).



Character state (0) is probably plesiomorphic, with Acrodonta having developed state (1). The basal condition of Scleroglossa is equivocal, but state (2) characterizes gekkotans, anguimorphs (except *Shinisaurus*), lacertoid

scincomorphs and *Trimeresurus*. The most parsimonious interpretation would be that scincoids have independently acquired state (0).



CHARACTER .55.

Also state (2) links lacertids and teiids, while state (3) is a derived feature for *Diplometopon* (the distribution of [3] in Amphisbaenia needs to be studied).

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56) The posterior intercentra (hypapophyses) muscle to the skull inserts on

(0) Basioccipital
(*Sphenodon, Shinisaurus*)
(1) Oto-occipital
(*Anolis, Crotaphytus, Oplurus, Agama,* gekkotans, *Gerrhosaurus,* anguids, varanids, *Diplometopon*)
(2) Basioccipital and oto-occipital
(*Phrynosoma, Iguana,* most dissected agamids [except *Agama*], chamaeleons, scincids, *Cordylus,* lacertids, teiids, *Heloderma, Trimeresurus*)
(3) Absent
(*Caiman*).

The polarity is problematic. Character state (2) seems to be basal for squamates; state (1) is shared by gekkotans, *Diplometopon,* and many anguimorphs (except

Shinisaurus, Heloderma and *Trimeresurus*). Pleurodont iguanians show variation and a broader survey would be needed.

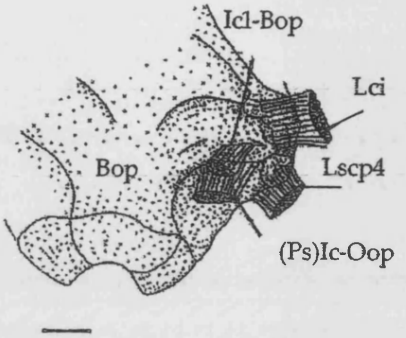
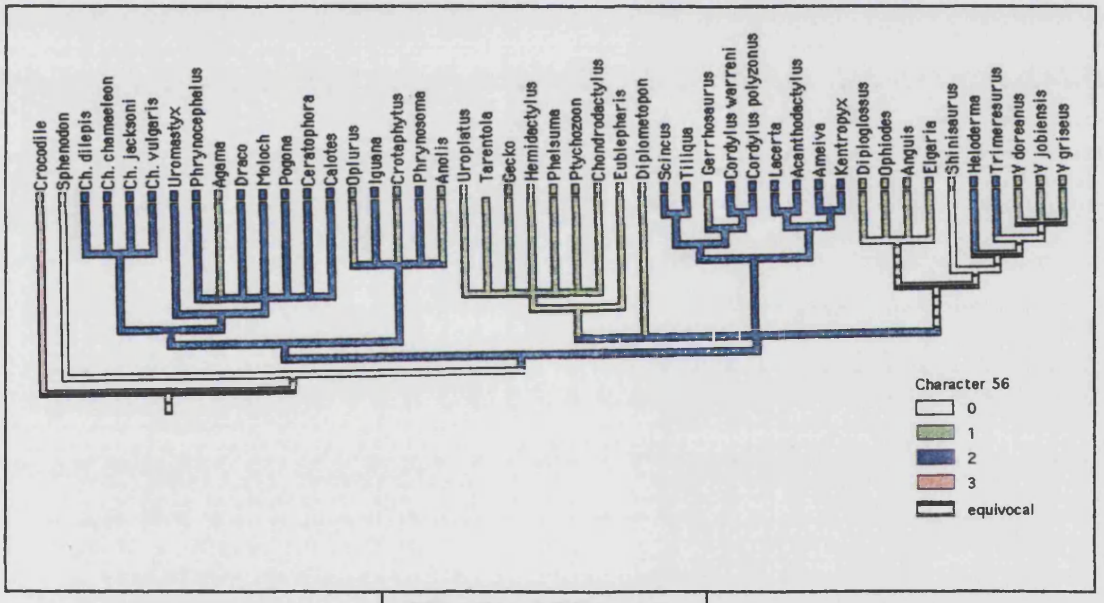


Fig. (10.7.38) *Gehyra marginata*, anteroventral view of the basioccipital showing the insertion of the posterior intercentral muscle slips on the oto-occipital ([Ps]Ic-Oop). Scale bar = 1 mm.

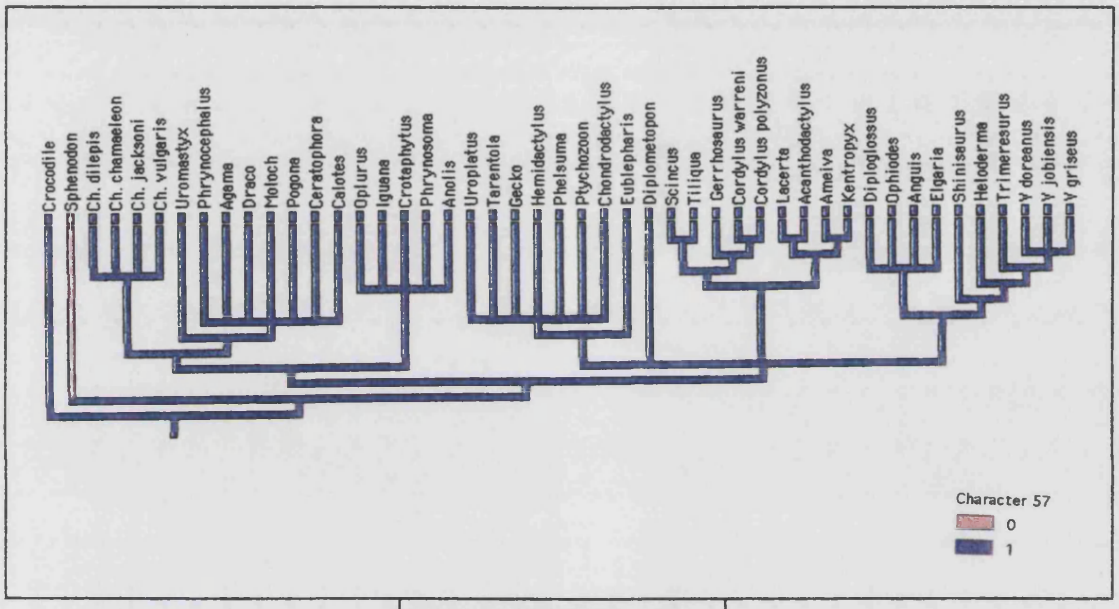


CHARACTER .56.

57) Presence or absence of axis to supraoccipital muscle

(0) Present
(*Sphenodon*)
(1) Absent
(*Caiman*, squamates)

The muscle is present only in *Sphenodon* where traces of muscle attachment are found on the superior side of the supraoccipital (bony crest) (0). According to Penning (1968), the equivalent muscle in mammals is rectus capitis posterior, while in birds the muscle has not been described (Berge and Zweers, 1993). Absence (1) is probably a synapomorphy of squamates, occurring independently in *Caiman* (further dissection of *Caiman* and other crocodiles is needed).



CHARACTER .57.

Osteological characters

58) Posterodorsal process of the parietal

(0) Absent (smooth)
(*Caiman*, *Sphenodon*, iguanids, agamids, lacertids, teiids, anguimorphs, *Trimeresurus*, *Diplometopon*)
(1) Reduced (small crest between two large squamosals)
(all chamaeleons examined)
(2) Present
(scincids, cordylids [forked], gekkotans)

The posterior margin of the parietal is smooth (0) in most of the taxa examined, but in scincids, cordylids and gekkotans the bone possesses a small median posterior process (2) (forked in cordylids – McDowell and Bogert, 1954; Jollie, 1960) (Fig., 10.7.39b). In chamaeleons the parietal is reduced and a small crest is exposed posteriorly in some of the species examined (1) (Fig., 10.7.39c).

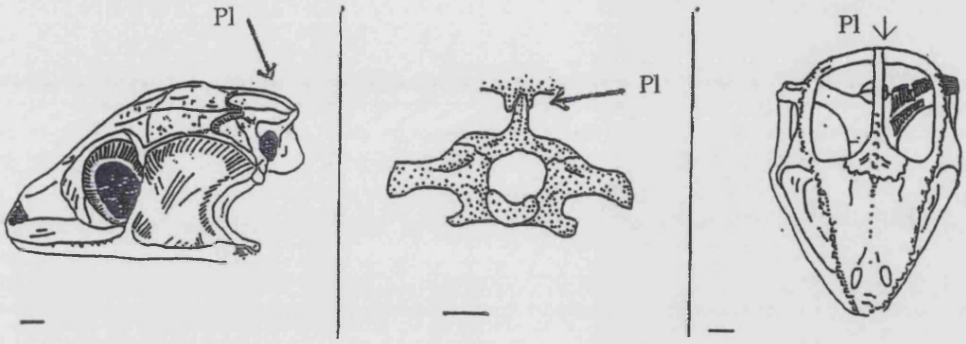
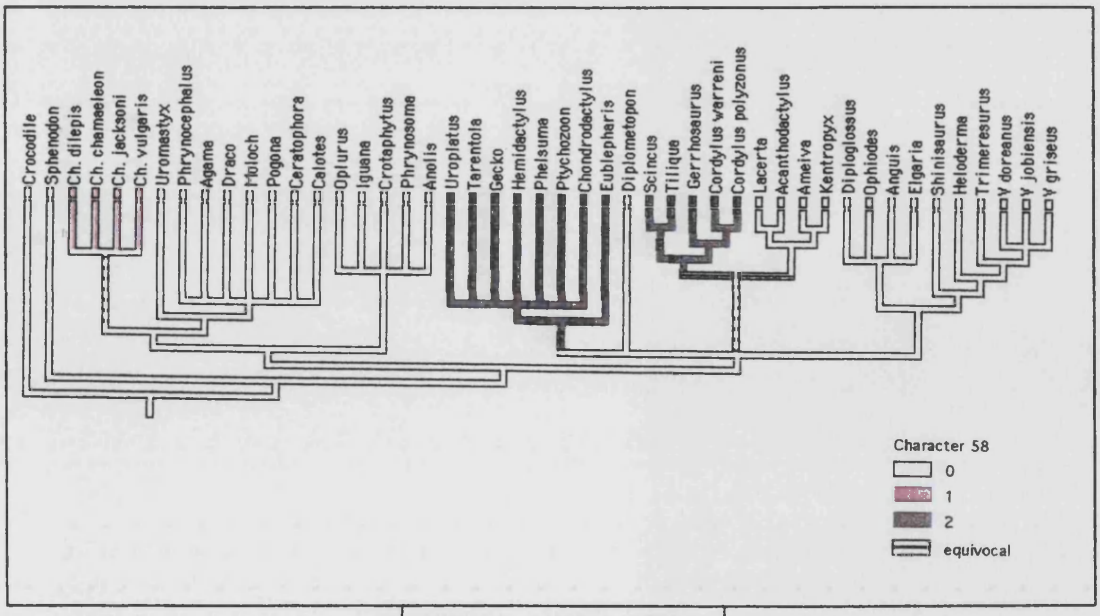


Fig. (10.7.39) a) *Ptychozoon kuhli*, left lateral view of the skull showing the posterodorsal process of the parietal (Pl). b) *Gerrhosaurus flavigularis*, occipital view of the skull showing the forked posterodorsal process of the parietal (Pl). c) *Chamaeleo chamaeleon*, dorsal view of the skull showing the reduced (rod-shaped) parietal (Pl). Scale bar = 1 mm.

This morphology in chamaeleons is related to the peculiar morphology of the casque. The process may be synapomorphy of scincids and cordylids, and also of Gekkota.

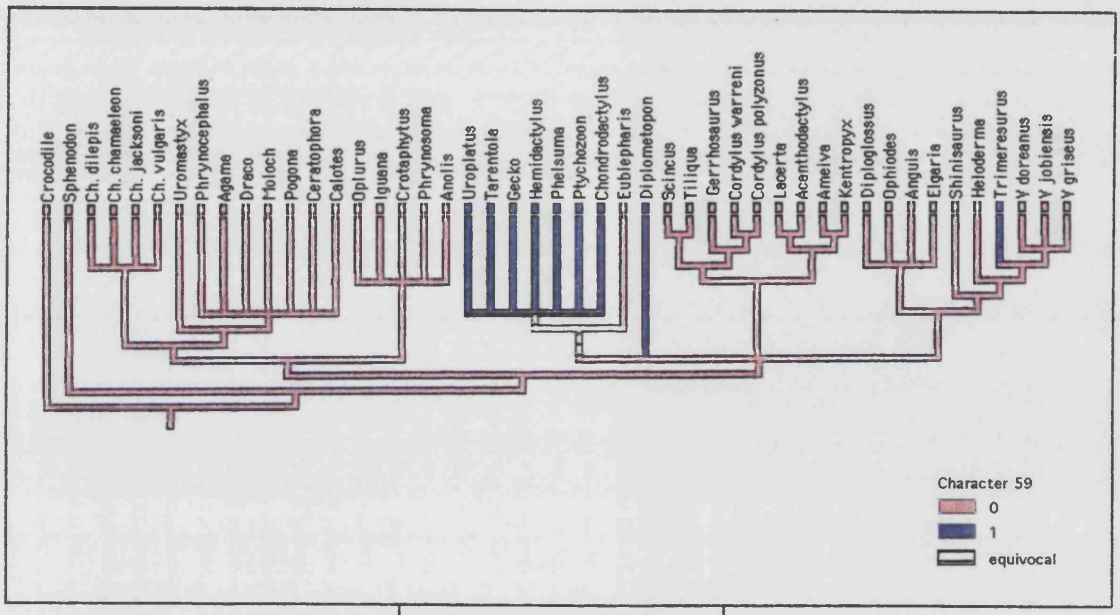


CHARACTER .58.

59) Presence or absence of the squamosal

(0) Present
(most groups examined)
(1) Absent
(gekkonids, *Diplometopon, Trimeresurus*)

The squamosal is present (0) in all amniotes. Loss of the squamosal (1) occurs in non-eublepharid gekkotans, in *Diplometopon* and snakes, probably independently (Romer, 1956).



CHARACTER .59.

60) The shape of the squamosal

(0) Quadriradiate
(*Caiman, Sphenodon*)
(1) Triradiate
(*Phrynosoma*, chamaeleons)
(2) Splint (narrow) (most squamates examined)

Character state (0) is plesiomorphic; and found in all primitive amniotes (Romer, 1956). Character state (2) is basal for squamates (e.g., varanids – Fig., 10.7.40b) while chamaeleons and some agamids possess state (1) (Fig., 10.7.40a), although all iguanians have a dorsal squamosal process.

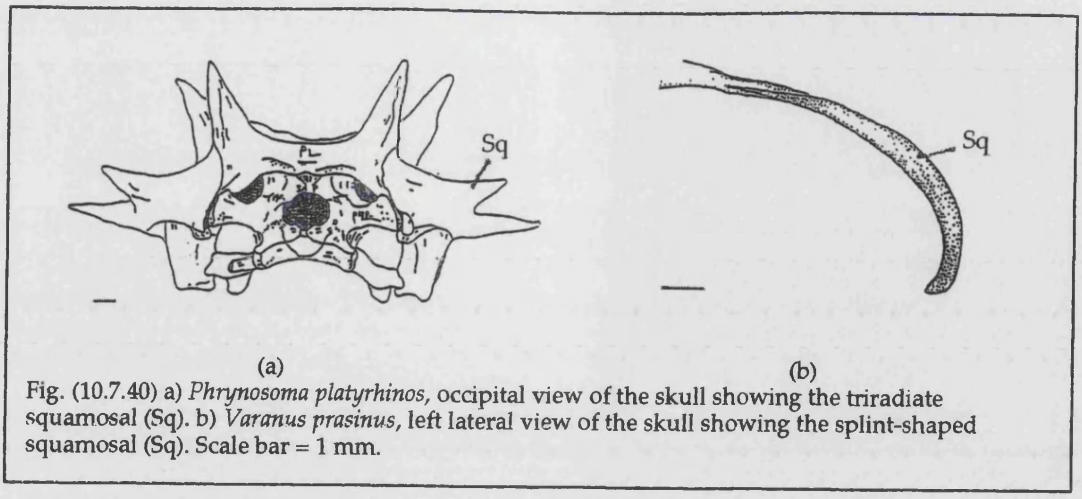
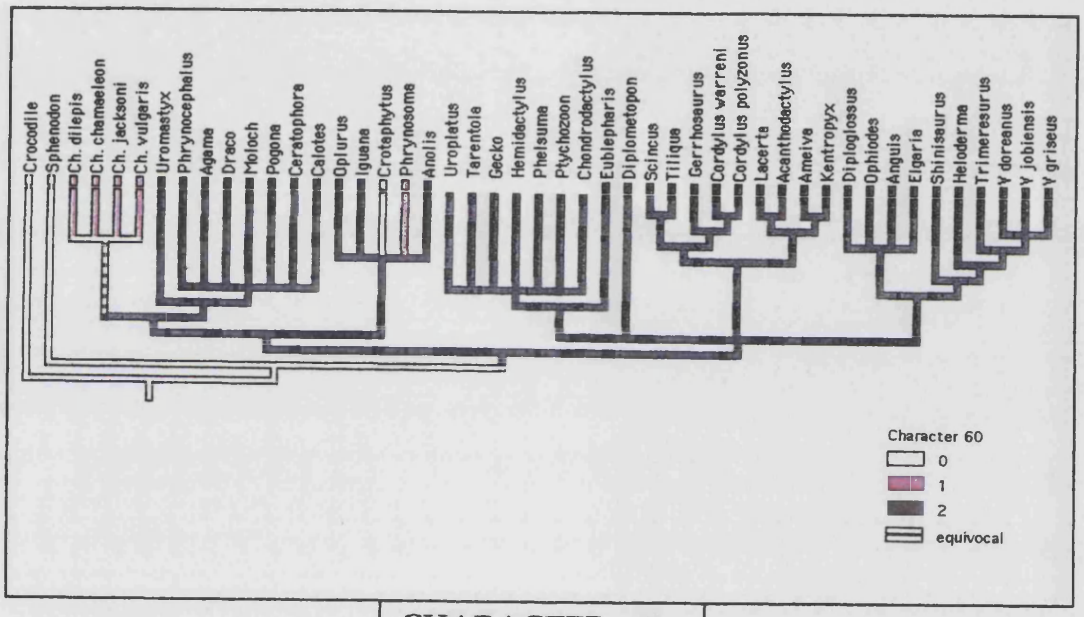


Fig. (10.7.40) a) *Phrynosoma platyrhinos*, occipital view of the skull showing the triradiate squamosal (Sq). b) *Varanus prasinus*, left lateral view of the skull showing the splint-shaped squamosal (Sq). Scale bar = 1 mm.



CHARACTER .60.

61) Presence or absence of squamosal dorsal process

(0) Present
(*Caiman*, *Sphenodon*, iguanians, many examined teiids)
(1) Absent
(scincids, lacertids, cordylids, eublepharids, anguimorphs)

Character state (0) is plesiomorphic and it probably persisted in basal squamates (Fig., 10.7.41) (Beddard, 1905; Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1997; Evans and Chure, 1998; Lee, 1998; Reynoso, 1998). State (1) is a

synapomorphy of Scleroglossa with reversal in many teiids (Estes et al., 1988). The absence of the dorsal process is correlated with a reduction in width of the upper temporal fenestra (scincids, lacertids, cordylids, eublepharids and anguimorphs), while the dorsal process tends to be retained in those groups in which the fenestra remains broad (Jollie, 1960). Estes et al (1988) suggested the process might have a role in bracing the posterior margin of the upper temporal fenestra,

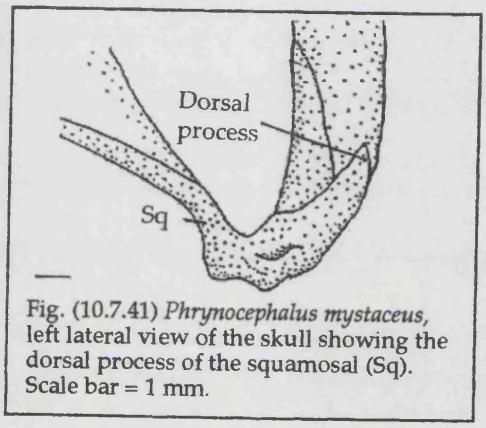
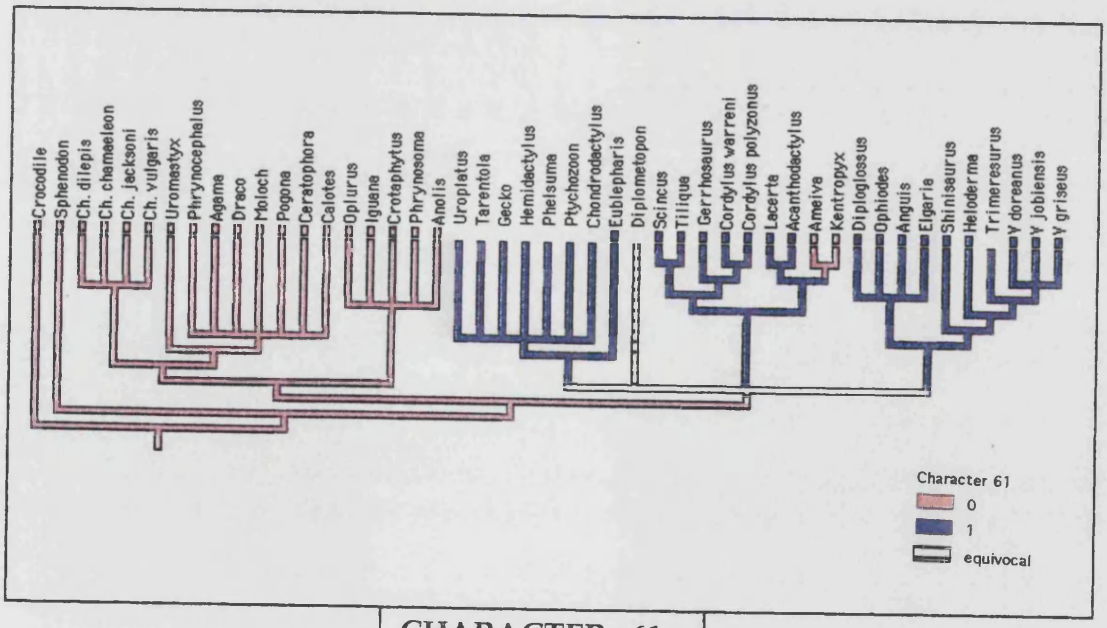


Fig. (10.7.41) *Phrynocephalus mystaceus*, left lateral view of the skull showing the dorsal process of the squamosal (Sq). Scale bar = 1 mm.



CHARACTER .61.

62) Presence or absence of supratemporal

(0) Present
(most examined squamates)
(1) Absent
(Caiman, Sphenodon, C. jacksonii)

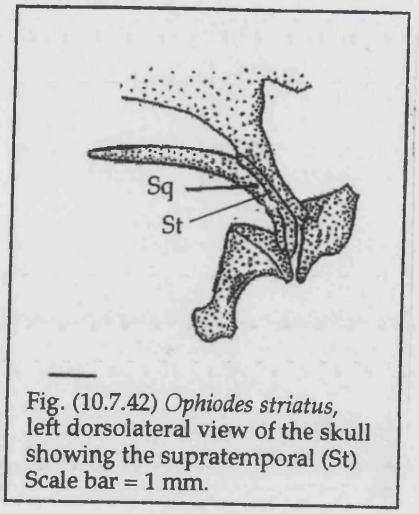
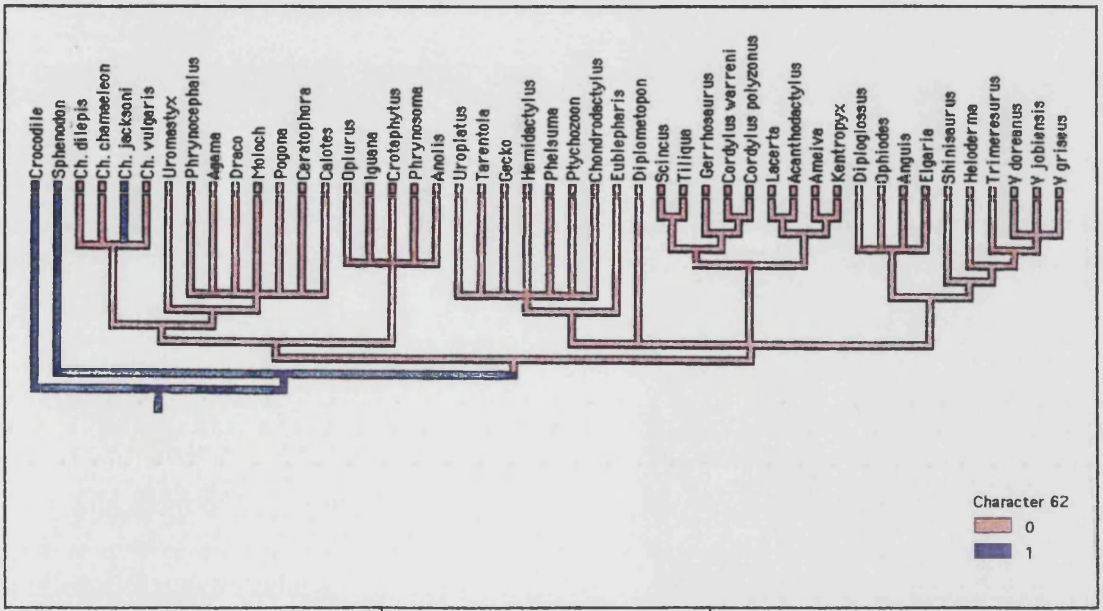


Fig. (10.7.42) *Ophiodes striatus*, left dorsolateral view of the skull showing the supratemporal (St) Scale bar = 1 mm.

A supratemporal is primitively present (0) in reptiles and their ancestors (Romer, 1956; Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1997; Evans and Chure, 1998). The supratemporal is retained in a majority of squamates (Fig., 10.7.42) because it has a role in the dorsal articulation for the quadrate (Jollie, 1960). The parietal posterolateral processes are lost in chamaeleons but most chamaeleons examined had a supratemporal except *Chamaeleo jacksonii*. The bone is absent in the adult *Sphenodon* but studies of development show that a supratemporal ossification is present in the hatching and becomes fused to the squamosal in the adult (Rieppel, 1993). Brock (1932) reported its absence in some gekkotans such as pygopodids, as well as some amphisbaenians (Zangerl, 1944) and *Dibamus* (Rieppel, 1984).



CHARACTER .62.

63) Location of basal tubera on the basioccipital

(0) Lateral
(most examined groups)
(1) Central
(Trimeresurus)

The location of the basal tubera on the lateral margin of the basioccipital is widely distributed and clearly plesiomorphic (0). In *Trimeresurus*, the tubera have shifted centrally (1). This shift seems to be correlated with the central attachment of longus colli on the basioccipital (Cundall and Greene, 2000 – Fig., 10.7.43). More dissection is needed to determine whether it is a derived feature of snakes generally.

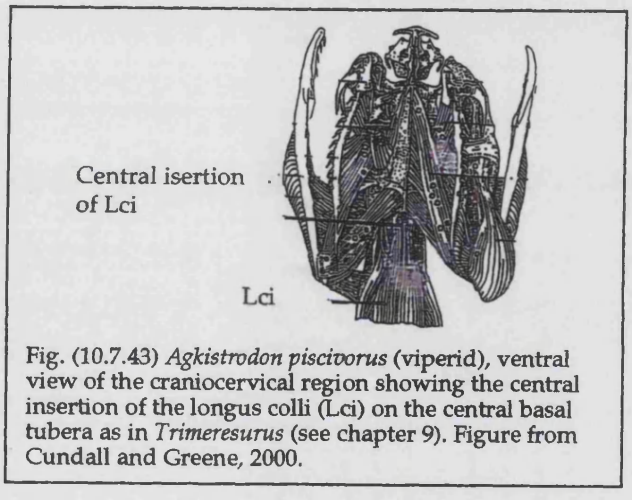
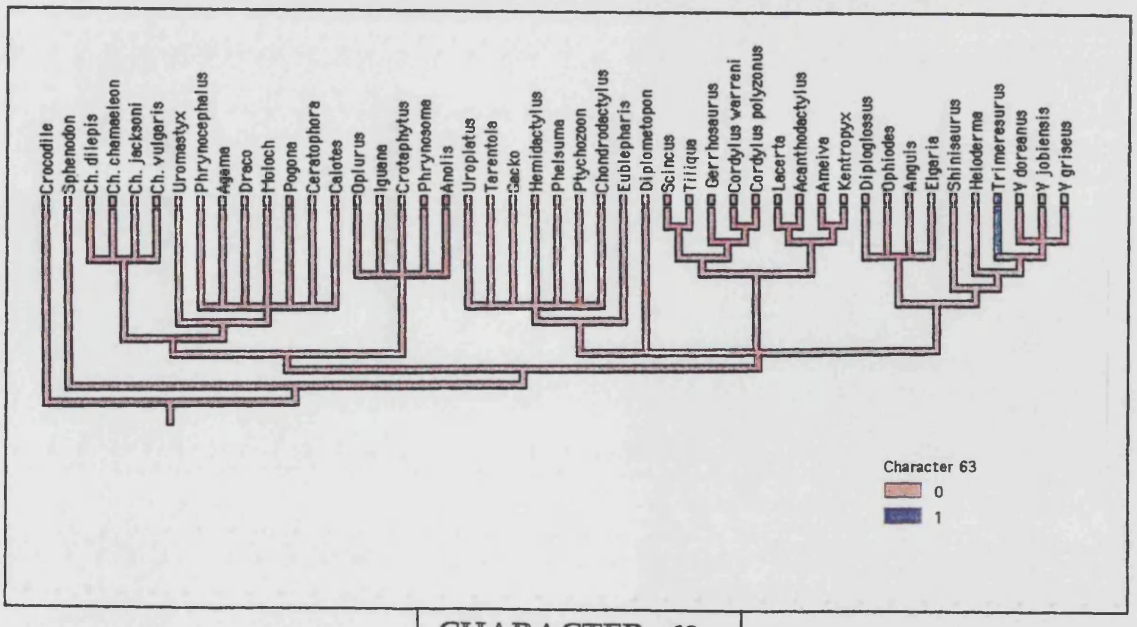


Fig. (10.7.43) *Agkistrodon piscivorus* (viperid), ventral view of the craniocervical region showing the central insertion of the longus colli (Lci) on the central basal tubera as in *Trimeresurus* (see chapter 9). Figure from Cundall and Greene, 2000.



CHARACTER .63.

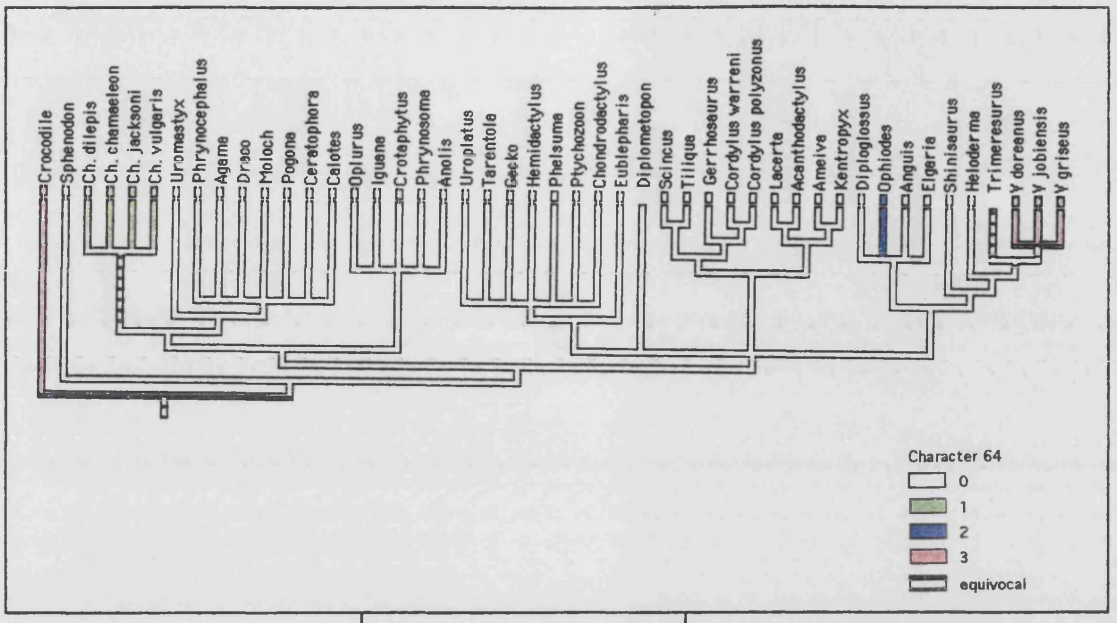
64) Number of cervical vertebrae

(0) Eight
(*Sphenodon*, iguanids, agamids, gekkotans, scincomorphs, anguids, *Shinisaurus*, *Heloderma*)
(1) Five
(chamaeleons)
(2) Six
(*Ophiodes* [anguids])
(3) Nine
(*Caiman*, varanids)

In chelonians, the cervical and trunk regions are easily distinguished although the sternum is absent (Hoffstetter and Gasc, 1969). They have 8 highly modified cervical vertebrae without ribs (Romer, 1956; Bellairs, 1969). Most mammals have 7 cervical vertebrae (Clemente, 1985; Agur et al., 1991; Warfel, 1993; Netter, 1998). The number of cervical vertebrae in living lepidosaurs ranges between 5-9, but 7-8 cervical vertebrae is the most widespread state (0), (Günther, 1867 – *Sphenodon* = C8; El-Toubi, 1947; Romer, 1956; Wu et al., 1996 - *Sineoamphisbaena*; Evans and Barbadillo, 1997 – *Scandensia ciervensis*; Lee, 1997; Evans and Chure, 1998; Reynoso, 1998 – *Huehuecuetzpalli*).

Shortening of the neck has occurred in chamaeleons as a result of the head stabilisation required for their special lifestyle (Bustard, 1963; Abu-Ghalyun et al., 1988; Wahaba et al., 1992b; Necas, 1999; Pleguezuelos et al., 1999).

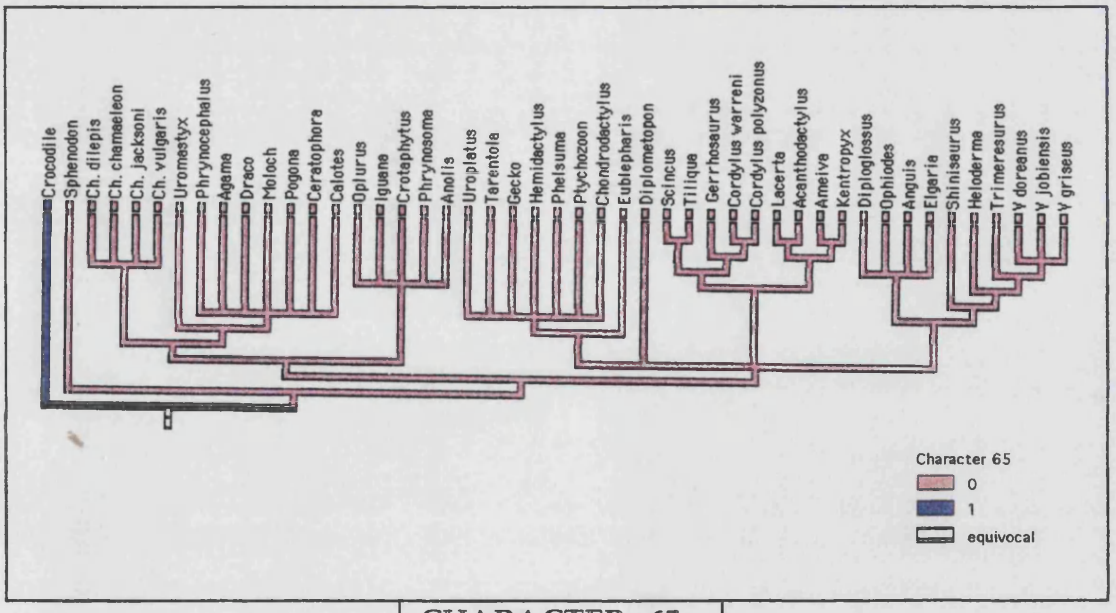
Elongation of the neck has occurred in *Caiman* (=C9 – Romer, 1956; Hoffstetter and Gasc, 1969; Frey, 1989), varanids, probably in response to their active predatory life style (a synapomorphy coded by Estes et al., 1988), and in *Lanthanotus* (C9, McDowell and Bogert, 1954). Further elongation of the neck has occurred in some extinct aquatic varanoids (Caldwell, 2000; Lee, 1997, 1998).



CHARACTER .64.

65) Presence or absence of intercentra

(0) Present
(*Sphenodon*, squamates)
(1) Absent
(*Caiman*)



CHARACTER .65.

The presence of intercentra throughout the vertebral column (0) is a primitive state found in basal reptiles (Boulenger, 1891; Romer, 1956; Evans, 1981; Estes et al., 1988; Wu et al., 1996; Evans and Barbadillo, 1997; Evans and Chure, 1998).

Intercentra were lost in the ancestors of derived archosaurs (e.g. *Caiman*), but retained in the earliest members of Lepidosauria. This condition is present in *Sphenodon*, but trunk intercentra were lost in the ancestors of squamates (retained in the neck and the tail). The absence of intercentra between dorsal vertebrae is the plesiomorphic condition in squamates (Estes et al., 1988; Hoffstetter and Gasc, 1969). Gekkotans and xantusiids are the only Scleroglossa to sometimes retain intercentra in the trunk region, and this is considered to be a derived feature (Kluge, 1967, 1983; Hoffstetter and Gasc, 1969; Estes et al., 1988; Gauthier et al., 1988) related to paedomorphosis. In helodermatids the intercentra are lost from the third and subsequent cervical vertebrae (Pregill et al., 1986; Estes et al., 1988; Gauthier et al., 1988).

66) Position of intercentra in relation to centra

(0) Between centra
(*Sphenodon*, gekkotans, most examined iguanids [except *Anolis*], *Uromastyx* [juvenile], *Chamaeleo chamaeleon*, *Scincus alifasciatus*, *Acanthodactylus*)
(1) Fused to centrum behind
(most examined agamids, most examined chamaeleons, teiids, *Lacerta*, cordylids)
(2) Fused to centrum in front
(*Anolis*, most examined scincids, anguimorphs, *Diplometopon*, *Trimeresurus*)

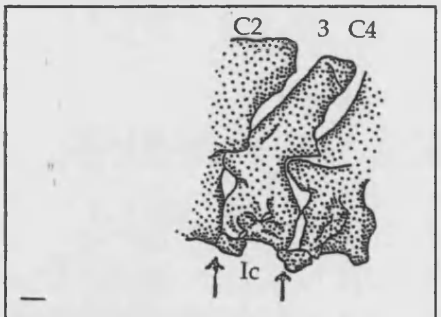


Fig. (10.7.44a) *Sphenodon*, right lateral view of the anterior vertebrae showing the intercentra (Ic) between centra. Scale bar = 1 mm.

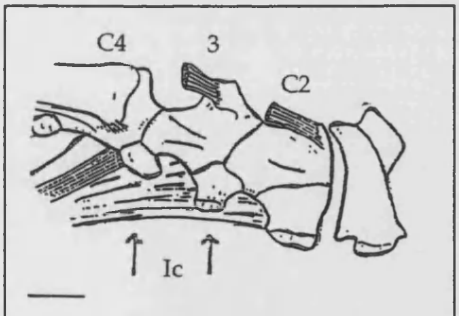


Fig. (10.7.44b) *Chamaeleo chamaeleon*, left ventrolateral view of the anterior vertebrae showing the intercentra (Ic) between centra. Scale bar = 1 mm.

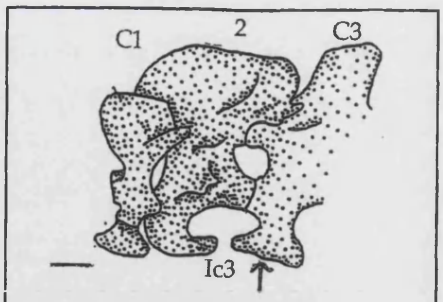


Fig. (10.7.44c) *Pseudocordylus microlepidotus*, right lateral view of the anterior cervical vertebrae showing the intercentra (Ic) fused to the centrum behind. Scale bar = 1

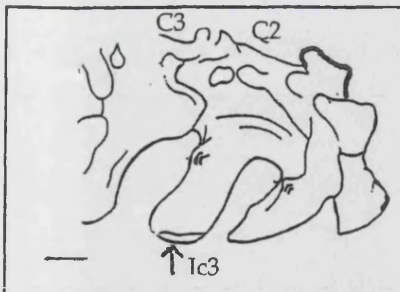
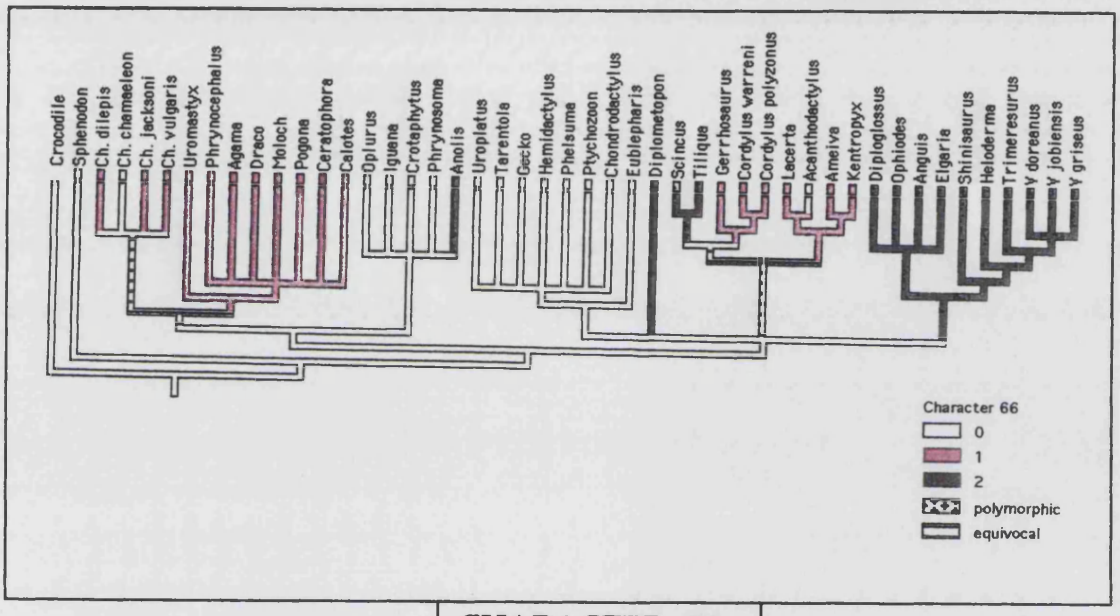


Fig. (10.7.44d) *Diploglossus shamini.*, right ventrolateral view of the anterior cervical vertebrae showing the intercentra (Ic) fused to the centrum in front. Scale bar = 1 mm.



CHARACTER .66.

The intercentra attach to the centrum behind (1) (Fig., 10.7.44c) (Hoffstetter and Gasc, 1969), in front (2) (Fig., 10.7.44d) (Hoffstetter and Gasc, 1967) or intercentrally (free) as in *Sphenodon* and gekkotans (0) (Hoffstetter and Gasc, 1969; Estes et al., 1988; Evans and Barbadillo, 1997 – *Meyasaurus*). The intercentra and centra are either sutured or fused. State (1) is a synapomorphy of Acrodonta, and perhaps of scincomorphs with a reversal in scincids (more taxa need to be dissected), However, Estes et al. (1988) reported this condition to be plesiomorphic in squamates, and this was supported by Reynoso (1998) who recorded it in the extinct primitive lizard *Huehuecuetzpalli mixtecus*. State (2) is a synapomorphy of anguimorphs, *Diplometopon* and *Trimeresurus*. The occurrence

of this feature in dibamids as well (Estes et al., 1988) may suggest a relationship between anguimorphs, amphisbaenians, snakes and dibamids. In most amphisbaenians the intercentra are completely fused to the preceding centrum (e.g. Trogonophinae – Gans, 1960), but those of *Sineoamphisbaena hexatabularis* are sutured or fused (Wu et al., 1996). The character shows some intra – and interspecific variation (see table for *Uromastyx* juvenile and adult; *Chamaeleo*, *Scincus*), and must be used with care when coding 0/1 or 0/2.

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67) The first cervical rib articulates on

(0) C1
(*Caiman*)
(1) C3
(*Sphenodon, Uroplatus*)
(2) C4
(*Crotaphytus, Phrynosoma, Ceratophora,* chamaeleons,

(*Sphenodon, Uroplatus*)
(2) C4
(*Crotaphytus, Phrynosoma, Ceratophora,* chamaeleons,
most examined gekkotans, scincomorphs, anguids, *Shinisaurus, Heloderma, Trimeresurus, Diplometopon*)
(3) C5
(*Oplurus, Anolis, Iguana,* most examined agamids,
(4) C6
(*Draco, Varanus griseus, Varanus gilleni*)
(5) C7
(*Varanus doreanus, Varanus jobiensis*)

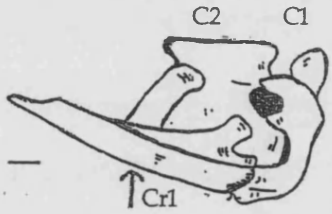
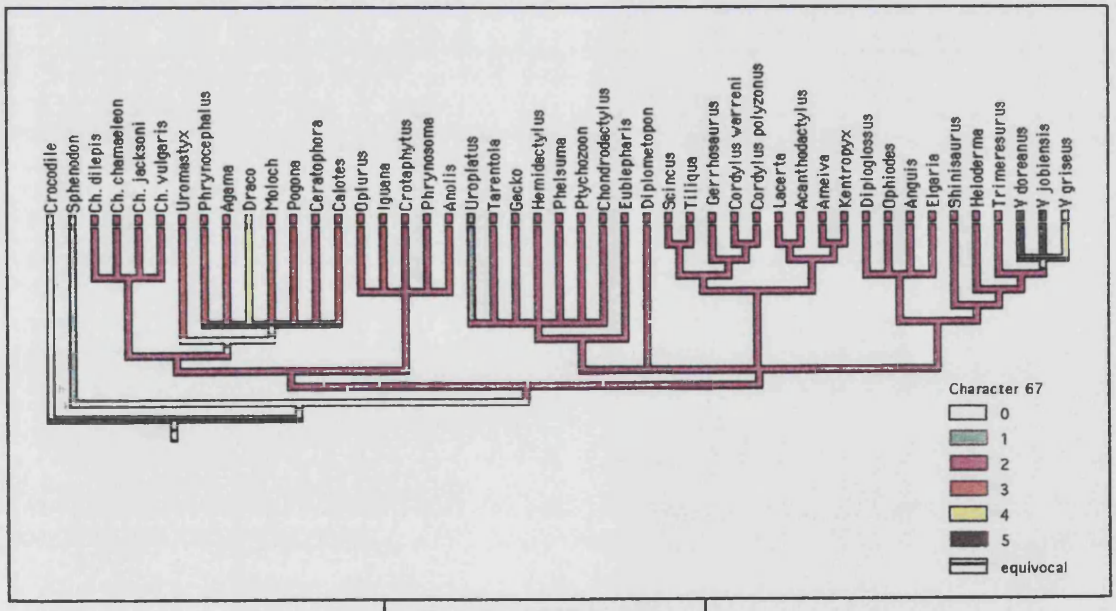


Fig. (10.7.45) *Caiman crocodilus*, right ventrolateral view of the atlas and axis showing the articulation of the 1st rib on the atlas (Cr1). Scale bar = 1 mm.

vertebra along the vertebral column (Romer, 1956). In subsequent lineages, there has been a tendency to lose ribs from some vertebral levels, especially in the neck. In the extinct mosasaurs, all the cervical vertebrae bear ribs except the atlas (Russell, 1967). *Caiman* shows the primitive condition in retaining a rib on the atlas and axis (0) (Fig., 10.7.45) (Camp, 1923). These atlantal and axial ribs were lost in early lepidosaurs although rarely they are regained (e.g. *Dibamus*, Estes et al., 1988). In *Sphenodon* and *Uroplatus* the first rib articulates on C3 (1). In agamids (e.g. *Uromastyx*

hardwickii - Tilak, 1964) and in iguanids (Etheridge, 1964; Moody, 1980; Etheridge and de Queiroz, 1988) the first rib is reported to articulate with C3, although most agamids and iguanids I examined had the first rib on C4 or C5. Most squamates have the first rib on C4 (Romer, 1956; Hoffstetter and Gasc, 1969; Estes et al., 1988; Evans and Barbadillo, 1997). In *Draco* and some varanids, ribs are absent on the first five cervical vertebrae, and the first cervical rib articulates on C6, while other varanids have the first cervical rib as far posteriorly as C7 (Hoffstetter and Gasc, 1969). Character states (4) and (5) shows interspecific variation within *Varanus* and should probably be combined into a single state (at or posterior to C6). In limbless forms such as Pygopodidae the number of ribless cervical vertebrae is reportedly either two or three (i.e. first rib articulates on C3 or C4) (Kluge, 1976), but in the amphisbaenian *Bipes*, the first rib attaches on C5 (Zangerl, 1945). In *Dibamus*, the atlas is the only ribless vertebrae, while the axis possesses a small free first rib (Gasc, 1967).



CHARACTER .67.

The polarity is problematic, with either state (2) or possibly (3) as the basal squamate condition.

Data matrix of muscle and bone characters

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	Sphenodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	Iguana	0	0	0	0	0	2	0	1	0	1	0	1	0	0	0	0	1	1	0	1	0
3	Crotaphytus	0	0	0	0	0	2	0	1	0	1	2	1	0	0	0	0	1	1	0	1	0
4	Phrynosoma	0	1	0	0	0	2	0	1	0	3	0	1	0	0	1	0	1	0	0	0	0
5	Oplurus	0	0	0	0	1	3	0	1	0	1	1	0	0	0	0	0	1	1	0	1	0
6	Anolis	0	1	0	0	0	2	0	1	2	3	0	1	0	0	0	0	1	1	0	1	0
7	Uromastyx	1	1	0	0	1	3	0	1	0	1	0&1	1	0	0	0	0	0	0	0	0	0
8	Draco	1	1	0	0	1	2	0	1	2	1	?	0	0	0	?	?	?	?	?	?	?
9	Calotes	1	1	0	0	1	2	0	1	2	1	1	1	0	0	?	?	?	?	?	?	?
10	Phrynocephalus	1	1	0	0	1	2	0	1	2	1	1	1	0	0	?	?	?	?	?	?	?
11	Agama	1	1	0	0	1	3	0	1	2	1	?	1	0	0	?	?	?	?	?	?	?
12	Ceratophora	1	1	0	0	1	2	0	1	2	1	?	1	0	0	?	?	?	0	0	0	?
13	Moloch	1	1	0	0	1	2	0	1	2	1	?	0	0	0	?	?	?	?	?	?	?
14	Pogona	1	1	0	0	1	3	0	1	2	1	?	1	0	0	?	?	?	0	0	0	?
15	Ch. chamaeleon	1	2	2	0	0	3	0	1	2	4	2	0	0	0	0	0	2	0	0	0	0
16	Ch. jacksoni	1	2	2	0	0	3	0	1	2	4	2	1	0	0	0	0	2	0	0	0	0
17	Ch. vulgaris	1	2	2	0	0	3	0	1	2	4	2	1	0	0	0	0	2	0	0	0	0
18	Ch. dilepis	1	2	2	0	0	3	0	1	2	4	2	0	0	0	0	0	2	0	0	0	0
19	Eublepharis	1	3	0	0	1	0	0	1	2	0	1	1	1	0	0	0	0	0	1	1	1
20	Uroplatus	2	2	0	0	1	0	0	1	2	1	1	0	1	0	1	1	0	0	1	2	1
21	Ptychozoon	0	3	0	0	1	0	0	1	2	1	1	1	1	0	0	0	0	0	1	2	1
22	Chondrodactylus	0	1	0	0	1	0	0	1	2	1	1	1	1	0	1	0	0	0	1	2	1
23	Hemidactylus	0	3	0	0	1	0	0	1	2	1	0	1	1	0	1	0	0	0	1	2	1
24	Tarentola	0	3	0	0	1	0	0	1	2	1	1	1	1	0	0	0	0	0	1	2	1
25	Gecko	0	1	0	0	1	0	0	1	2	1	1	1	1	0	0	0	0	0	1	2	1
26	Phelsuma	0	3	0	0	1	0	0	1	2	1	1	1	1	0	0	0	0	0	1	2	1
27	Scincus	0	1	0	0	1	0	0	1	1	1	1	1	0	1	1	2	0	0	1	0	0
28	Tiliqua	1	1	0	0	1	0	0	1	1	3	1	0	0	0	0	0	0	0	0&1	0	0
29	Lacerta	1	3	0	0	1	0	0	1	1	3	1	0	0	0	0	0	0	0	0	0	0
30	Acanthodactylus	1	3	0	0	1	0	0	1	1	3	1	1	0	0	0	0	0	0	0	0	0
31	Ameiva	1	3	0	0	1	0	0	1	1	3	1	1	0	0	0	0	0	0	0	0	0
32	Kentropyx	1	3	0	0	1	0	0	1	1	3	0	1	0	0	0	0	0	0	0	0	0
33	Cordylus polyzonus	1	1	0	0	1	0	0	1	1	3	1	1	0	0	0	0	0	0	0	0	0
34	Cordylus warreni	1	1	0	0	1	0	0	1	1	3	1	1	0	0	0	0	0	0	0	0	0
35	Gerrhosaurus	1	1	0	0	1	0	0	1	1	1	1	1	0	1	1	0	0	0	0	0	0
36	V jobiensis	2	1	0	1	1	3	0	1	2	2	2	1	1	0	0	0	0	1	1	2	1
37	V doreanus	2	1	0	1	1	3	0	1	2	2	2	1	1	0	0	0	0	1	1	2	1
38	V griseus	2	1	0	1	1	3	0	1	2	2	2	1	1	0	0	0	0	1	1	2	1
39	Heloderma	?	?	0	0	1	?	0	1	2	2	?	?	1	0	0	?	0	0	?	2	?
40	Shinisaurus	1	1	0	0	1	1	0	1	2	1	2	1	1	0	0	0	0	1	0	2	1
41	Ophiodes	1	1	0	0	1	1	0	1	2	2	1	0	1	0	0	0	0	0	1	2	?
42	Anguis	1	1	0	0	1	1	0	1	2	2	?	0	1	0	0	0	0	0	0	2	?
43	Elgaria	1	1	0	0	1	1	0	1	2	1	2	1	1	0	0	0	0	0	0	2	?
44	Diploglossus	1	?	0	0	1	1	0	1	2	?	2	1	1	0	0	0	0	0	0	2	?
45	Diplometopon	3	1	1	0	1	4	1	1	2	4	2	?	1	0	0	0	0	0	?	2	0
46	Trimeresurus	4	3	0	0	1	4	1	1	3	5	2	?	1	0	0	0	0	0	?	0	0
47	Crocodile	1	0	0	0	1	1	0	0	4	4	2	0	1	1	0	0	0	0	1	1	0

		22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
1	Sphenodon	0	1	0	0	0	0	0	0	?	0	1	0	0	0	0	1	0	0	0	0	0
2	Iguana	0	1	0	0	0	0	0	1	0	1	1	1	1	0	1	1	1	0	0	1	4
3	Crotaphytus	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	4
4	Phrynosoma	0	1	0	1	0	3	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1
5	Oplurus	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
6	Anolis	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1
7	Uromastyx	0	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	1	1
8	Draco	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	4
9	Calotes	0	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	0	1
10	Phrynocephalus	0	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	1	1
11	Agama	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1
12	Ceratophora	0	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1	0	0	0	1	4
13	Moloch	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	2
14	Pogona	0	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1
15	Ch. chamaeleon	0	1	0	2	0	1	0	1	0	1	1	0	1	1	2	1	0	0	2	?	?
16	Ch. jacksoni	0	1	0	2	0	1	0	1	0	1	1	0	1	1	2	1	0	0	2	?	?
17	Ch. vulgaris	0	1	0	2	0	1	0	1	0	1	1	0	1	1	2	1	0	0	2	?	?
18	Ch. dilepis	0	1	0	2	0	1	0	1	0	1	1	0	1	1	2	1	0	0	2	?	?
19	Eublepharis	0	1	0	0	1	0	1	1	1	1	1	1	1	1	2	1	1	0	0	1	2
20	Uroplatus	0	1	0	0	1	0	1	1	1	1	1	0	0	1	2	1	1	0	0	0	3
21	Ptychozoon	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
22	Chondrodactylus	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
23	Hemidactylus	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
24	Tarentola	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
25	Gecko	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
26	Phelsuma	0	1	0	0	1	0	1	1	1	1	1	1	0	1	2	1	1	0	0	1	3
27	Scincus	1	1	0	0	0	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	1
28	Tiliqua	0	1	0	0	0	1	1	1	0	1	1	0	1	0	2	1	0	0	0	1	1
29	Lacerta	0	1	0	0	0	1	1	1	1	1	1	0	1	1	2	1	0	0	0	1	1
30	Acanthodactylus	0	1	0	0	0	1	1	1	1	1	1	0	1	1	2	1	0	0	0	1	1
31	Ameiva	0	1	0	0	0	1	1	1	1	1	1	1	1	1	2	1	0	0	0	1	2
32	Kentropyx	0	1	0	0	0	1	1	1	1	1	1	1	1	1	2	1	0	0	0	1	2
33	Cordylus polyzonus	0	1	0	0	0	1	1	1	1	1	1	1	1	0	2	1	0	0	0	1	1
34	Cordylus warreni	0	1	0	0	0	1	1	1	1	1	1	1	1	0	2	1	0	0	0	1	1
35	Gerrhosaurus	0	1	0	0	0	1	1	1	1	1	1	1	1	0	2	1	1	0	0	1	1
36	V jobiensis	0	1	0	0	0	0	1	1	2	1	1	1	0	1	2	1	0	1	1	0	5
37	V doreanus	0	1	0	0	0	0	1	1	2	1	1	1	0	1	2	1	0	1	1	0	5
38	V griseus	0	1	0	0	0	0	1	1	2	1	1	1	0	1	2	1	0	1	1	0	5
39	Heloderma	0	1	0	0	0	0	1	1	?	1	1	1	1	1	2	1	0	0	1	1	5
40	Shinisaurus	0	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	0	1	1	4
41	Ophiodes	0	1	0	0	0	0	1	1	?	1	1	0	1	1	2	1	1	0	0	1	1
42	Anguis	0	1	0	0	0	0	1	1	1	1	1	1	1	1	2	1	1	0	?	?	?
43	Elgaria	0	1	0	0	0	0	1	1	1	1	1	1	1	1	2	1	0	0	1	1	4
44	Diploglossus	0	1	0	0	0	0	1	1	1	1	1	0	1	1	2	1	1	0	0	1	1
45	Diplometopon	0	1	1	1	0	0	1	0	?	1	1	?	1	1	2	2	1	0	1	1	3
46	Trimeresurus	0	1	0	0	0	2	1	0	?	1	1	?	0	1	2	1	1	0	2	?	?
47	Crocodile	0	0	0	0	0	0	1	0	?	?	0	0	0	1	1	0	1	0	2	?	?

		43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
1	Sphenodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2	Iguana	0	1	1	1	1	0	2	0	1	0	0	0	0	2	1	0	0	2	0	0	0
3	Crotaphytus	0	1	1	1	1	0	2	0	1	1	0	0	0	1	1	0	0	0	0	0	0
4	Phrynosoma	0	1	2	1	1	0	3	0	?	1	0	0	0	2	1	0	0	1	0	0	0
5	Oplurus	0	1	2	1	1	0	2	0	1	0	0	0	0	1	1	0	0	2	0	0	0
6	Anolis	0	1	2	1	1	0	2	0	1	0	0	0	0	1	1	0	0	2	0	0	0
7	Uromastyx	0	1	2	1	1	0	2	0	1	1	0	0	1	2	1	0	0	2	0	0	0
8	Draco	0	1	2	1	1	0	4	0	?	0	0	0	1	2	1	0	0	2	0	0	0
9	Calotes	0	1	1	1	1	0	1	0	?	0	0	0	1	2	1	0	0	2	0	0	0
10	Phrynocephalus	0	1	1	1	1	0	2	0	?	1	0	0	1	2	1	0	0	2	0	0	0
11	Agama	0	1	1	1	1	0	2	0	?	0	0	0	1	1	1	0	0	2	0	0	0
12	Ceratophora	0	1	2	1	1	0	2	0	?	1	0	0	1	2	1	0	0	2	0	0	0
13	Moloch	0	1	1	1	1	0	1	0	?	1	0	0	1	2	1	0	0	2	0	0	0
14	Pogona	0	1	1	1	1	0	2	0	?	0	0	0	1	2	1	0	0	2	0	0	0
15	Ch. chamaeleon	?	?	?	1	1	0	3	0	0	1	0	0	1	2	1	1	0	1	0	0	0
16	Ch. jacksoni	?	?	?	1	1	0	1	0	0	1	0	0	1	2	1	1	0	1	0	1	0
17	Ch. vulgaris	?	?	?	1	1	0	2	0	0	1	0	0	1	2	1	1	0	1	0	0	0
18	Ch. dilepis	?	?	?	1	1	0	2	0	0	1	0	0	1	2	1	1	0	1	0	0	0
19	Eublepharis	0	0	1	0	1	1	1	0	0	0	0	0	2	1	1	2	0	2	1	0	0
20	Uroplatus	0	0	1	0	1	1	2	0	1	0	0	0	2	1	1	2	1	?	?	0	0
21	Ptychozoon	0	0	1	0	1	1	2	0	1	0	0	0	2	1	1	2	1	?	?	0	0
22	Chondrodactylus	0	0	1	0	1	1	2	0	1	0	0	0	2	1	1	2	1	?	?	0	0
23	Hemidactylus	0	0	1	0	1	1	2	0	1	0	0	0	2	1	1	2	1	?	?	0	0
24	Tarentola	0	0	1	0	1	1	?	0	1	0	0	0	2	?	1	2	1	?	?	0	0
25	Gecko	0	0	1	0	1	1	2	0	1	0	0	0	2	1	1	2	1	?	?	0	0
26	Phelsuma	0	0	1	0	1	1	1	0	1	0	0	0	2	1	1	2	1	?	?	0	0
27	Scincus	0	1	2	1	1	0	2	0	1	1	0	0	0	2	1	2	0	2	1	0	0
28	Tiliqua	0	1	2	1	1	0	2	0	1	1	0	0	0	2	1	2	0	2	1	0	0
29	Lacerta	0	1	2	1	1	0	2	0	1	1	0	0	2	2	1	0	0	2	1	0	0
30	Acanthodactylus	0	1	2	1	1	0	2	0	1	1	0	0	2	2	1	0	0	2	1	0	0
31	Ameiva	0	1	2	1	1	0	3	0	1	1	0	0	2	2	1	0	0	2	0	0	0
32	Kentropyx	0	1	2	1	1	0	?	0	1	1	0	0	2	2	1	0	0	2	0	0	0
33	Cordylus polyzonus	0	1	2	1	1	0	2	0	1	1	0	0	0	2	1	2	0	2	1	0	0
34	Cordylus warreni	0	1	2	1	1	0	2	0	1	1	0	0	0	2	1	2	0	2	1	0	0
35	Gerrhosaurus	0	1	2	1	1	0	2	0	1	1	0	0	0	1	1	2	0	2	1	0	0
36	V jobiensis	1	1	0	0	0	2	2	1	1	1	1	1	2	1	1	0	0	2	1	0	0
37	V doreanus	1	1	0	0	0	2	2	1	1	1	1	1	2	1	1	0	0	2	1	0	0
38	V griseus	1	1	0	0	0	2	2	1	1	1	1	1	2	1	1	0	0	2	1	0	0
39	Heloderma	0	?	1	0	0	0	0	0	0	1	0	0	?	2	1	0	0	2	1	0	0
40	Shinisaurus	1	1	2	0	0	1	2	0	0	1	0	0	0	0	1	0	0	2	1	0	0
41	Ophiodes	0	1	2	0	0	1	3	0	0	0	0	1	2	1	1	0	0	2	1	0	0
42	Anguis	?	?	?	0	0	1	2	0	0	0	0	0	2	1	1	0	0	2	1	0	0
43	Elgaria	1	1	2	0	1	1	3	0	0	0	0	0	2	1	1	0	0	2	1	0	0
44	Diploglossus	0	1	2	0	1	1	3	0	0	0	0	1	2	1	1	0	0	2	1	0	0
45	Diplometopon	1	1	2	0	1	2	4	0	1	1	0	0	3	1	1	0	1	2	?	0	0
46	Trimeresurus	?	?	?	0	0	0	4	0	0	1	0	0	2	2	1	0	1	2	?	0	1
47	Crocodile	?	?	?	0	1	?	?	0	1	1	0	0	0	3	1	0	0	0	0	1	0

		64	65	66	67
1	Sphenodon	0	0	0	1
2	Iguana	0	0	0	3
3	Crotaphytus	0	0	0	2
4	Phrynosoma	0	0	0	2
5	Oplurus	0	0	0	3
6	Anolis	0	0	2	3
7	Uromastyx	0	0	1	3
8	Draco	0	0	1	4
9	Calotes	0	0	1	3
10	Phrynocephalus	0	0	1	3
11	Agama	0	0	1	3
12	Ceratophora	0	0	1	2
13	Moloch	0	0	1	3
14	Pogona	0	0	1	3
15	Ch. chamaeleon	1	0	0	2
16	Ch. jacksoni	1	0	1	2
17	Ch. vulgaris	1	0	1	2
18	Ch. dilepis	1	0	1	2
19	Eublepharis	0	0	0	2
20	Uroplatus	0	0	0	1
21	Ptychozoon	0	0	0	2
22	Chondrodactylus	0	0	0	2
23	Hemidactylus	0	0	0	2
24	Tarentola	0	0	0	2
25	Gecko	0	0	0	2
26	Phelsuma	0	0	0	2
27	Scincus	0	0	0&2	2
28	Tiliqua	0	0	2	2
29	Lacerta	0	0	1	2
30	Acanthodactylus	0	0	0	2
31	Ameiva	0	0	1	2
32	Kentropyx	0	0	1	2
33	Cordylus polyzonus	0	0	1	2
34	Cordylus warreni	0	0	1	2
35	Gerrhosaurus	0	0	1	2
36	V jobiensis	3	0	2	5
37	V doreanus	3	0	2	5
38	V griseus	3	0	2	4
39	Heloderma	0	0	2	2
40	Shinisaurus	0	0	2	2
41	Ophiodes	2	0	2	2
42	Anguis	0	0	2	2
43	Elgaria	0	0	2	2
44	Diploglossus	0	0	2	2
45	Diplometopon	?	0	2	2
46	Trimeresurus	?	0	2	2
47	Crocodile	3	1	?	0

Summary

Craniocervical characters and major clades

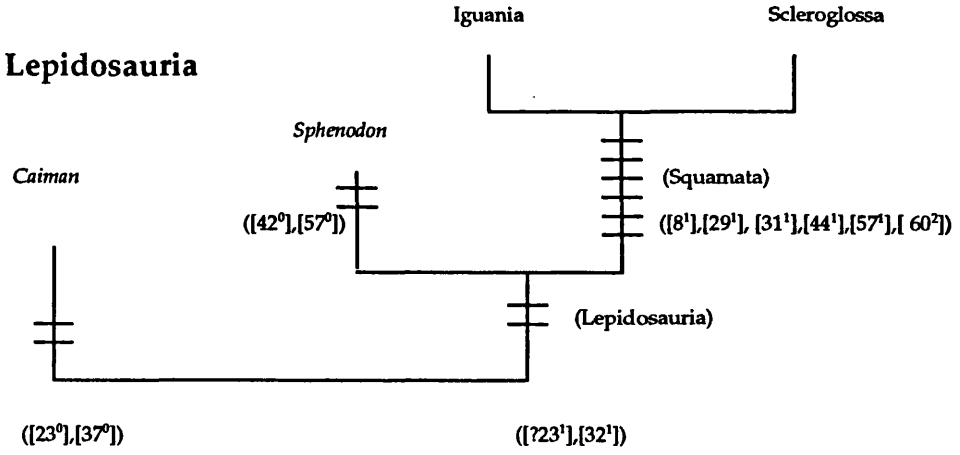
The distribution of anatomical characters outlined above provides support for the monophyly of some major clades.

Note: the bold characters represent characters with intra/and interspecific variation. ? = unsure about the character state (primitive or derived) or/and polarity is unclear.

Lepidosauria (Rhynchocephalia and Squamata) is supported by [?23^1] and[32^1].

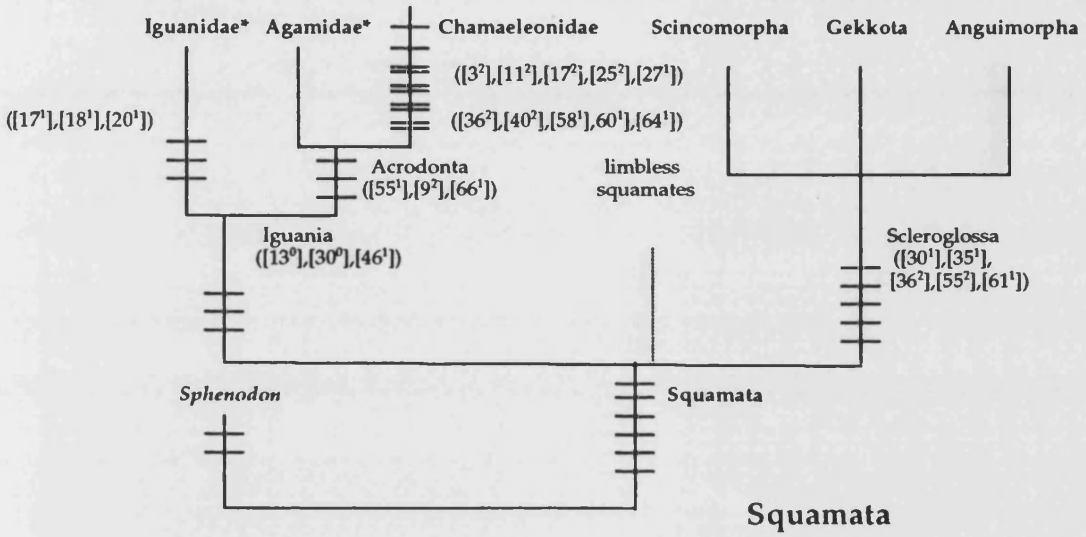
Rhynchocephalia (*Sphenodon punctatus*) is the closest relative and first out-group to squamates (Estes et al., 1988; Gauthier et al., 1988; Evans, 1991). *Sphenodon* has unique craniocervical features ([42^0], [57^0]).

Squamata (iguanians, Scleroglossa – Estes et al., 1988; Gauthier et al., 1988) was supported by [8^1]; [?31^1]; [57^1] and [60^2]. Moreover, characters [29^1] and [44^1] are shared by most squamates.



Iguania (Iguanidae*, Agamidae*, Chamaeleonidae) is the sister group to Scleroglossa (Estes et al., 1988; Gauthier et al., 1988; Lee, 1998). Iguania share features ([13^0], [?30^0] and [46^1]). Characters [17^1], [18^1] and [20^1] are shared by most Iguanidae*, while character [36^1], and [35^0] are shared by Iguanidae* and

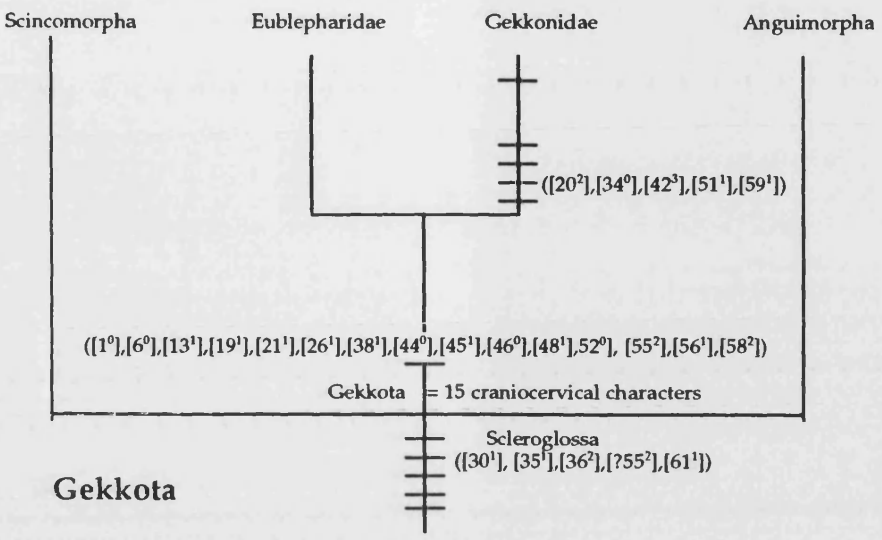
Agamidae*. Character [**55**^{1}] supports the monophyly of Acrodonta (agamids and chamaeleonids) (Camp, 1923; Moody, 1980; Rieppel, 1981), and characters [?9^{2}] and [**66**^{1}] are also shared by most Acrodonta. All Chamaeleonidae* examined (i.e. 4 species belonging to one genus *Chamaeleo*) share features ([3^{2}], [**11**^{2}],[17^{2}], [25^{2}], [27^{1}], [36^{2}], [40^{2}], [58^{1}], [60^{1}] and [64^{1}]).



Scleroglossa (Scincomorpha, Gekkota, Anguimorpha – Estes et al., 1988) was supported by character (61) with exceptions in teiids. Scleroglossa also shares several characters such as [30^{1}], [?35^{1}], [**?55**^{2}] and [36^{2}].

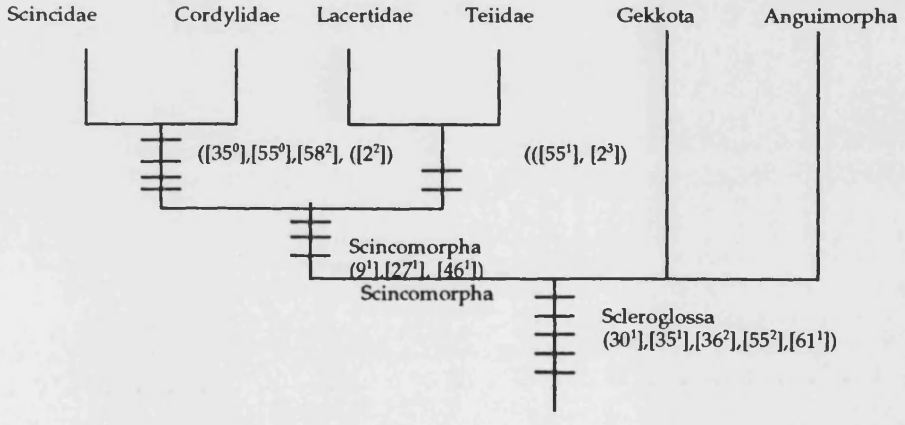
Gekkota (Gekkonidae, Eublepharidae) they share one unique craniocervical muscular feature ([26]^{1}). Other characters that support gekkotan monophyly but are also found in other groups are [1^{0}], [6^{0}], [13^{1}], [**19**^{1}], [21^{1}], [38^{1}], [44^{0}], [45^{1}], [46^{0}], [48^{1}], [52^{0}], [55^{2}], [56^{1}] and [58^{2}].

Gekkonids together share several craniocervical features ([20^{2}], [34^{0}], [42^{3}], [?51^{1}], [59^{1}]). *Uroplatus fimbriatus* has two crainocervical unique muscular features [2^{2}] and [16^{1}].



Scincomorpha (Scincidae, Cordylidae, Lacertidae, Teiidae) share only one unique craniocervical feature ([9¹]) that supports the monophyly of Scincomorpha (has a wide insertion of episternocleidomastoid on skull shelf). However, the longissimus capitis 2 inserts as L-shaped on paroccipital process in most Scincomorpha, while characters [27¹] and [46¹] are shared by all scincomorphs and some iguanians.

Scincidae and Cordylidae are linked by characters [2¹], [58²] and, potentially, by [35⁰], and [?55⁰], but only if these are reversals (Scincoidea – Estes, 1983; Estes et al, 1988; 1998; Rieppel, 1988; Evans and Chure, 1998; Hallerman), while Lacertidae and Teiidae share character [2³] and [55¹] (Lacertoidea – Camp, 1923; Saint Girons, 1970; Estes, 1983; Estes et al, 1988; Rieppel, 1988; Hallerman, 1998).



features with Gekkonidae ([42^3]); with gekkonids and anguimorphs (([20^2]); with Gekkonidae and snakes ([59^1]); and with varanids ([48^2]). *Diplometopon* shared character [11^2] with Anguimorpha as both have clavicle and both lack the clavicle dorsalis muscle. Also *Diplometopon* shares traits with most limbed Anguimorpha ([40^1] and [43^1]); with Gekkota, Anguimorpha and *Trimeresurus* ([13^1]); and with the snake *Trimeresurus* ([6^4], [7^1] and [29^0]), but this is probably due to convergence.

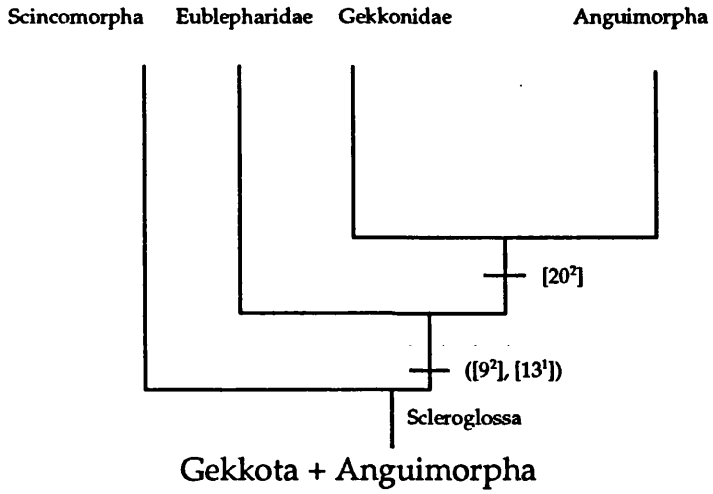
Serpentes (*Trimeresurus wagleri*) This limbless squamate has some unique craniocervical features ([9^3], [27^2], [63^1]), but shares many scleroglossan characters. With varanids it shares one character ([34^0]), with Gekkonidae and *Diplometopon* ([59^1]) and with gekkotans, Anguimorpha and *Diplometopon* ([13^1]).

Relationship between major clades of Scleroglossa and the position of the limbless squamates *Diplometopon* and *Trimeresurus*:

A) Gekkota, Scincomorpha and Anguimorpha:

Gekkota shares characters with both Scincomorpha and Anguimorpha, but its position with respect to these groups remains unresolved. However, slightly more craniocervical characters link Gekkota with Anguimorpha than Scincomorpha. Character [6^0] links Gekkota and Scincomorpha (trapezius inserts on the suprascapula and clavicle), and character [58^2] links Gekkota and scincoids. However, characters [9^2], [13^1] and [20^2] unite most Gekkota and Anguimorpha, moreover, characters [21^1] and [48^1] link Gekkota with a subset of anguimorphs.

Gekkota and Anguimorpha



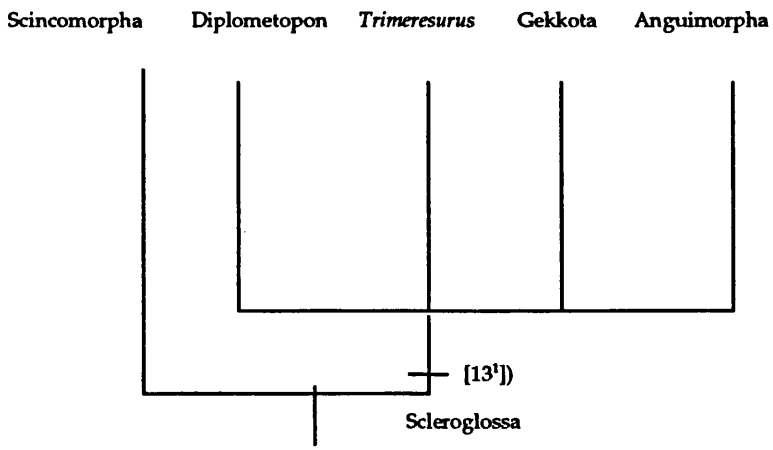
Gekkota + Anguimorpha

B) Position of limbless squamates to Scleroglossa:

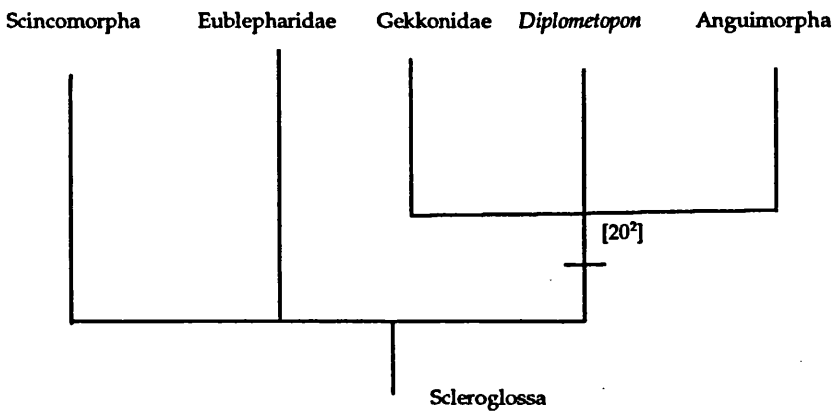
Craniocervical characters nested *Diplometopon* close to Gekkota (characters [20²], [42³] and [59¹] as proposed by Underwood, 1957; Caldwell, 1998; Lee, 1998; Reynoso, 1998) or to Anguimorpha (characters [40¹], [43¹] and [48²] as proposed by Rieppel and Zaher, 2000).

Amphisbaenians and relatives:

Diplometopon, *Trimeresurus*, Gekkota and Anguimorpha:



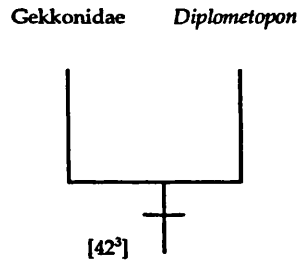
Diplometopon, Gekkonidae and Anguimorpha:



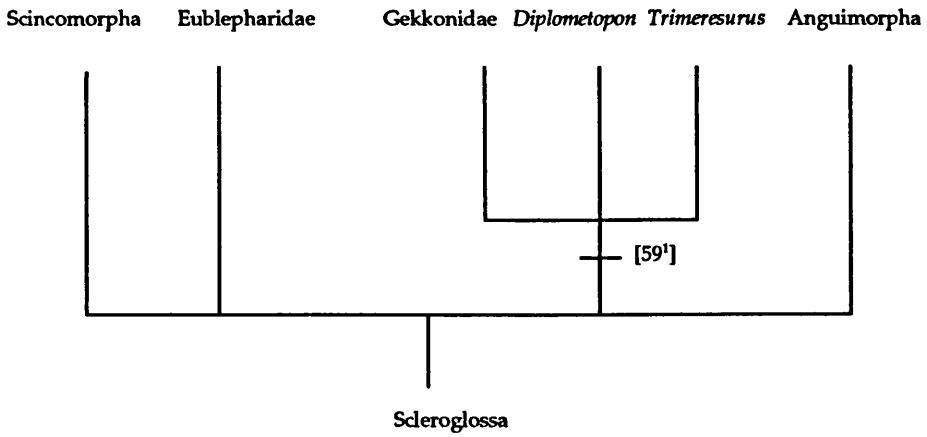
1- *Diplometopon* + Gekkota

(Supported by: Underwood, 1957; Caldwell, 1998; Lee, 1998; Reynoso, 1998)

- *Diplometopon* and Gekkonidae:



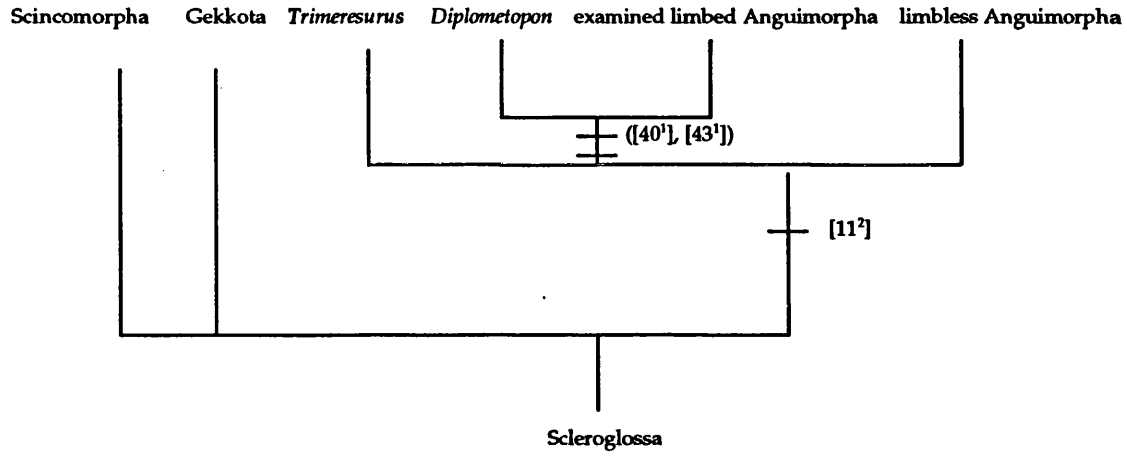
- *Diplometopon*, Gekkonidae and *Trimeresurus:*



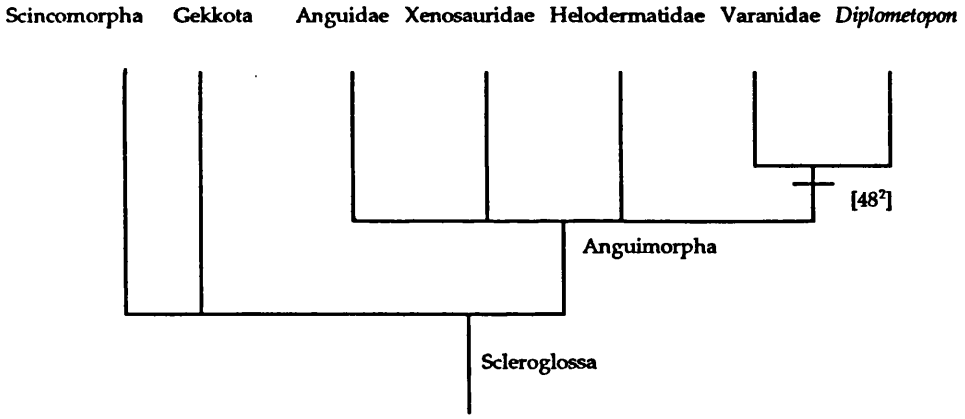
2- *Diplometopon* + Anguimorpha

(Supported by Rieppel and Zaher, 2000)

- *Diplometopon*, Anguimorpha and *Trimeresurus* = [11^2]
- *Diplometopon* and most limbed Anguimorpha = [40^2], [43^1]

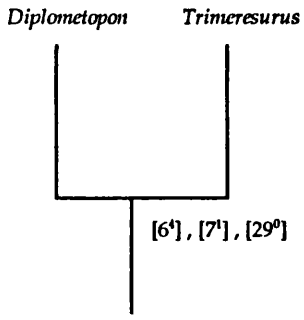


- *Diplometopon* and varanids



3- *Diplometopon* + *Trimeresurus*

(Supported by: Hellerman, 1998; Rieppel and Zaher, 2000; Tchernov et al., 2000)



IV - CONCLUSIONS

1) In reptiles, osteological features of the craniocervical region can be related to the presence or absence, size, position and mode of attachment of craniocervical muscles. Minor features are often subject to intra- and interspecific variation. However, together these bony features may be useful in understanding the functional morphology of extinct organisms.

2) There is a relationship between patterns of cranial kinesis and the pattern of origin and insertion of muscles on the occipital surface of the skull. Many craniocervical muscles insert on the occipital region of the skull. In Scleroglossa, there are more muscles inserting on the dorsal and lateral skull roof than on the braincase. This may reflect active metakinesis. Akinetic chamaeleons are exceptional: there are few muscles attaching to the skull roof, while numbers inserting on the braincase are dramatically high. These may operate to fix the skull to the neck rather than moving the skull.

3) Features of the ventral surface of the anterior presacral vertebral column may assist in the recognition of the boundary between the cervical and dorsal regions these include: the presence of the mid-ventral ridge of the centra; presence of lateral crests on the anterior vertebrae (where longus cervicus attaches); length and position of attachment of rib ligaments (where longus colli and cervicus attach); and shape of the rib distal ends (wide or forked). However the

transition between posterior cervicals and anterior dorsals is not sharp.

Unfortunately, these features do not help with amphisbaenians (e.g. *Diplometopon*) or snakes (e.g. *Trimeresurus*). In the limbless anguimorph *Ophiodes* the central ridge appears after the last keeled intercentra (where longus colli originates and the cervical region ends). Other features like presence of central bony processes, the presence or absence of intercentra and the presence or absence of basal crests is of less importance in characterising the neck region.

4) There are differences between the atlas/axis regions within lepidosaurs: the presence of a proatlas in *Sphenodon* is reflected by the presence of an anterior branch of the longissimus cervicus, and a tendinous sheet that connects the proatlas to the skull. The atlas/axis neural arch zygapophysial articulation is lost in squamates, and is replaced by a thick muscular connection.

5) The pectoral girdle is linked to the skull, cervical and dorsal vertebrae by superficial and intermediate muscles. The presence and position of attachment of such muscles reflects the presence or absence of appendicular elements. There are some craniocervical features linked to the presence of the pectoral girdle muscles (e.g. forked distal end of cervical ribs and special intercentral apices).

6) Most of the craniocervical features in limbless lizards like *Ophiodes* are similar to those of other squamates, while specialised limbless squamates like amphisbaenians (e.g. *Diplometopon*) and snakes (e.g. *Trimeresurus*) share derived features (for example, reduction of skull

bones and the presence of rib processes). Amphisbaenians are distinguished by differences in some deep craniocervical muscles (e.g., elongation and division of splenius capitis). These features combine with modifications of the skull and presacral vertebral column and may be related to digging and the subterranean mode of life. Several muscular characters distinguish snakes (for example, intrinsic quadrate muscles and parapophyses muscles). These features assist in increasing kinetic capacity and locomotion.

The degree of reduction of some anatomical features in the craniocervical region of limbless squamates probably reflects the time since limb loss (e.g., reduction or absence of longus cervicus).

7) In Squamata, there are some craniocervical muscles (like obliquus capitis, splenius capitis, longissimus capitis 1 and longus cervicus) that show discrete variations in their origin and insertion; branching; elongation; and thickness. Those features appear to characterise major groups like Iguanidae [17^1, 18^1]; Gekkota [26^1, 44^0]; Anguimorpha [40^1]; and *Diplometopon* [1^3, 3^1, 24^1, 25^1, 55^3].

8) However many muscle characters show intra and interspecific variation and are therefore too labile to be used in phylogenetic analysis.

9) Craniocervical features support the monophyly of Lepidosauria (1 or 2 characters); Squamata (5-6 characters) and Scleroglossa (1-5 characters), as well as the monophyly of major clades like Iguania (2-3 characters); Gekkota (12-15 characters); Scincomorpha (2-3); and Anguimorpha (6-9 characters), as well as that of Scincoidea (1-3

characters) and Lacertoidea (1 character). Anguids + Xenosauridae (2 characters); Varanidae + Xenosauridae (1 character); Varanidae + Helodermatidae (1 character). Acrodonta shared 1-3 characters, although some show intraspecific variation.

10) Within Squamata, craniocervical features suggest that Gekkota is closer to Autarchoglossa (Scincomorpha + Anguimorpha) than to Iguania, but there is a greater similarity between Gekkota and Anguimorpha, than with Scincomorpha. Autarchoglossa as a group is unresolved.

11) On balance, craniocervical features place amphisbaenians (*Diplometopon*) closer to Gekkota and possibly Anguimorpha than Scincomorpha. The place of Serpentes (*Trimeresurus*) within scleroglossans is unresolved, but character [34°] uniquely links *Trimeresurus* and varanids.

Future work

Furthered dissection is needed to decide the primitive amniote condition for many characters (e.g. of turtles and primitive mammals), with dissection of more crocodile species and birds to understand the distribution of craniocervical features within diapsids.

Iguania

Iguanidae* = more dissection from subfamilies like Tropidurinae, Hoplocercinae and Crotaphytinae (to compare with the specimens from the other five subfamilies). Dissection of *Chalarodon* (*C. madagascariesis)* to compare with *Oplurus cyclurus*. Dissection of the only living marine iguanid *Amblyrhynchus* in order to study the functional morphology of the neck.

Agamidae*: further dissection of agamids and more investigation of the dorsal and lateral sides of the craniocervical region (to compare with other iguanians and understand character distribution within Acrodonta).

Chamaeleonidae: dissection of other genera like *Brookesia* and *Bradypodion* in order to compare with *Chamaeleo* and understand character distribution in the family.

Gekkota

Eublepharidae = dissect more specimens

Pygopodidae = (*Pygopus; Delma; Lialis; Pletholax; Ophidiocephalus, Aprasia*)

Dissection of some genera of these limbless gekkotans to compare with other families (Gekkonidae and Eublepharidae). Some pygopodids retain hind limbs (paddle-like or flap footed) (Kluge, 1976, Bauer, 1992).

Scincomorpha

Dissection of more specimens of Scincidae, Cordylidae, Teiidae and Lacertidae, also more limbless Scincidae (e.g. Acontininae, Feylinae), limbless or nearly limbless cordylids (e.g. *Tetradactylus*), and gymnophthalmids to compare them to teiids. A dissection of Xantusiidae is needed to compare with other scincomorphs and gekkotans.

Anguimorpha

Dissection more specimens of Anguidae, Xenosauridae, and Varanidae. A dissection of *Anniella* is needed to compare with other limbless taxa of the subfamily Anguinae, as well as further dissection of Diploglossinae and Gerrhonotinae including the dorsal and lateral sides of the craniocervical region.

Dissection of *Xenosaurus* to compare with *Shinisaurus*, and a dissection of *Heloderma horridum*, dorsal and lateral sides of the craniocervical region, (with *Heloderma suspectum* for comparison).

The dissection of *Lanthanotus borneensis* as the sister taxon of Varanidae would be useful to understand character distribution.

Limbless squamates

It would be interesting to dissect more limbless squamates generally. Of all reduced limbed forms, it would be useful to examine those taxa with rudimentary and fore-limbs (e.g. the gymnophthalmid *Bachia*) or hind

limbs (e.g. *Pygopus* and skinks like *Scelotes*), to compare with completely limbless and limbed relatives.

Dibamids have been regarded as closely related to anguids, geckos, pygopodids, skinks, amphisbaenians or snakes (Baur, 1992). My results show some similarities between amphisbaenians, gekkotans, snakes and anguimorphs. It would be interesting to dissect dibamids (e.g. genus *Dibamus* and *Anelytropsis*) to compare with possible relatives.

Only one snake was dissected, the advanced arboreal *Trimeresurus*, but it would be important to dissect some primitive snakes like Anomalepididae, Typhlopidae and Leptotyphlopidae ("wormsnakes"), which show adaptations to burrowing.

The dissected amphisbaenian was *Diplometopon* (family Trogonophidae), but other amphisbaenians need to be studied (e.g. *Bipes*; other Trogonophidae with remnants of the pectoral girdle; and representatives of families like Rhineuridae [*Rhineura*] and Amphisbaenidae [*Blanus*]).

V - BIBLIOGRAPHY

Abdala, V., and Moro. S., 1996. Cranial musculature of South American Gekkonidae. *Journal of Morphology*, 229: 59-70.

Abu-Ghalyun Y., Greenwald, L., Hetherington, T. E., and Gaunt, A. S., 1988. The physiological basis of slow locomotion in chamaeleons. *Journal of Experimental Zoology*, 245: 225-231.

Agur, A. M. R., Lee, M.J., and Anderson, J. E., 1991. *Grants Atlas of Anatomy*. Baltimore, The Williams & Wilkins Co., ninth edtion. 252 pp.

Albrecht, P., 1883. Note sur la présence d'un rudiment de proatlas sur un exemplaire de *Hatteria punctata* Gray. *Bulletin du musée royale d'Histoire naturelle de Belgique*, 2: 185-192.

Alexander, R. McN., 1968. *Animal mechanics*. Sidgwick & Jackson, London, 346 pp.

Alifanov, V., 1993. The Upper Cretaceous lizard fauna of Mongolia, and the problem of the first interamerican contact. *Paleontological Journal*, 1993: 79-85.

Al-Nasser, N. A., 1976. *Anatomical studies: osteology and gut histology of the amphisbaenian Diplometopon zarudnyi inhabiting Kuwait*.Msc thesis, Kuwait University Press, Kuwait. 173 pp.

Arnold, E. N., 1981. Estimating phylogenies at low taxonomic levels. *Journal of Zoological Systematics and Evolutionary Research*, 19: 1-35.

----, 1984. Variation in the cloacal and hemipenial muscles of lizards and its bearing on their relationships. pp. 47-85. In, Ferguson, M. W. J. (ed.), *The structure, development and evolution of reptiles*. Symposia of the Zoological Society of London 52. Academic Press, London.

Auffenberg, W., 1962. A review of the trunk musculature in the limbless land vertebrates, *American Zoologist*, 2: 183-190.

Bahl, K. N., 1937. Skull of *Varanus monitor*. *Records of the Indian Museum*, 39: 133-74.

Baird, I. L., 1970. The anatomy of the reptilian ear. pp. 193-275. In, Gans, G. and Parsons, T.S. (ed.), *Biology of the Reptilia.* Volume 2, New York, Academic Press.

Barbadillo, L.J., and Barahona, F., 1994. The number of cervical vertebrae in lacertid lizards. Some unusual cases. *Herpetological Journal*, 4: 166.

Barrows, S., and Smith, H. M., 1947. The skeleton of the lizard *Xenosaurus grandis. University of Kansas Science Bulletin*, 31(12): 227-281.

Bauer, A. M. 1992. Lizards. pp. 126-174. In, Cogger, H.G. and Zweifel, R.G. (ed.), *Encyclopedia of Reptiles and Amphibians*. Part 3, Academic Press, USA.

Baur, G. Von., 1886. Osteologische Notizen über Reptilien. *Zoologischer Anzeiger*, 9(238): 685-690.

Beck, D. D., and Lowe, C. H., 1991. Ecology of the beaded lizard, *Heloderma horridum*, in a tropical dry forest in Jalisco. *Mexico Journal of Herpetology*, 25: 395-406.

Beddard, F. E., 1905. Some notes on the cranial osteology of the Mastigure Lizard, *Uromastyx. Proceedings of the Zoological Society, London*, 1905: 2-9.

Bekele, A., 1983. The comparative functional morphology of some head muscles of the rodents *Tachyoryctes splendens* and *Rattus rattus*. II. Cervical muscles. *Mammalia*, 47(a): 549-72.

Bellairs, A. d'A., 1969. *The Life of Reptiles,'* Volume 1 and 2. London: Weidenfeld & Nicolson. 590pp.

----, 1972. Comments on the evolution and affinities of snakes. pp. 72-157. In . Joysey, K. A. and Kemp, T. S. (ed.), *Studies in Vertebrate Evolution*. Oliver & Boyd, Edinburgh.

----, and Underwood, G., 1951. The origin of snakes. *Biological Reviews*, Cambridge Philosophical Society, 26: 193-237.

Benton, M. J., 1982. The diapsid revolution in reptile relationship. *Nature*, London, 296: 306-307.

----, 1985. Classification and phylogeny of the diapsid reptiles. *Zoological Journal of the Linnean Society*, 84: 97-164.

----, and Clark, J. M. 1988. Archosaur phylogeny and relationships of the Crocodylia. pp. 295-338. In, Benton M.J. (ed.), *The phylogeny and Classification of the Tetrapods, Volume 1: Amphibians, Reptiles, Birds.* Systematics Association Special Clarendon Press, Oxford.

Berge. J. C. and Zweers, G. A., 1993. Myologia. pp 189-247, In Baumel, J.S. (ed.), *Handbook of Avian Anatomy: Nomina Anatomica Avium.* Edition 2, Published: Nuttal Ornithological Club, 23 Cambridge, Massachusetts.

Blanc, C. P., 1965. Etudes sur les Iguanidae de Madagascar. Le squelette de *Chalarodon madagascariensis. Mémoires du Museum Nationale dHistoire Naturelles*, Paris, 33(3): 93-145.

Boulenger, G. A., 1891. Notes on the osteology of *Heloderma horridum* and *H. suspectum*, with remarks on the systematic position of the Helodermatidae and on the vertebrae of the Lacertilia. *Proceeding Zoological Society London*, 1891: 109-118.

Brock, G. T. 1932. The skull of the Leptotyphlops (*Glauconia nigricans*) *Anatomischer Anzeiger*, 73: 199-204.

----, 1941. The skull of *Acontias meleagris*, with a study of the affinities between lizards and snakes. *Journal of Linnean Society London*, 41: 71-88.

Broom, R. 1925. On the origin of lizards. *Proceedings of the Zoological Society of London*, 1925: 1-16.

Bustard, H.R. 1963. Growth sloughing, feeding, mating, gestation, life-span and poor health of Chamaeleons in captivity, *Copeia* 1963: 704-706.

Byerly, T. C. 1925. The myology of *Sphenodon punctatus. University of Iowa Studies in Natural History*, 11: 1-50.

Caldwell M.W. 1998. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society*, 125: 115-147.

----, 2000. On the aquatic squamate *Dolichosaurus longicollis*, (Cenomarian, Upper Cretaceous), and the evolution of elongate necks in squamates. *Journal of Vertebrate Paleontology*, 20: 720-735.

----, and Lee, M. S. Y. 1997. A snake with legs from the marine Cretaceous of the Middle East, *Nature* 386: 705-709.

Camp, C. L. 1923. Classification of the lizards. *Bulletin of the American Museum of Natural History*, 48: 289-481.

Carroll, R. L. 1970. The ancestory of reptiles. *Philosophical Transactions of the Royal Society. Biological Sciences*, (814): 267 – 308.

----, 1976. Eosuchians and the origin of archosaurs. *Miscellaneous Publications of the Life Sciences Division of the Royal Ontario Museum*, 1976: 58-79.

----, 1988. Late Paleozoic and Early Mesozoic lepidosauromorphs and their relation to lizard ancestry. pp. 99-118. In Estes, R. and Pregill, G., *Phylogenetic Relationships of the Lizard Families*, Stanford University Press, Stanford, California.

Clemente, C. D. 1985. *Gray's Anatomy.* 30 edition. Philadelphia, Lea and Febiger. 1676 pp.

Cleuren, J. and De Vree, F. 2000. Feeding in Crocodilians. pp. 337 – 357. In, Schwenk, K., (ed.), *Feeding*. Academic Press, London.

Coates, M. I. 1996. The Devonian tetrapod *Acanthostega gunneri*: postcranial anatomy, basal tetrapod interrelationships and patterns of skeletal evolution. *Tranaction of the Royal Society of Edinburgh, Earth Sciences*, 87: 363-421.

Cogger, H. G. and Zweifel, R. G. 1998. *Encyclopedia of Reptiles and Amphibians*. Second edition. Academic Press, USA. 240 pp.

Colbert, E. H. and Mook, C. C. 1951. The ancestral crocodilian *Protosuchus. Bulletin of the American Museum of Natural History*, 97: 147-192.

Cope, E. D., 1892. The osteology of the Lacertilia. *Proceeding of the American Philosophical Society*, 30: 185-222.

Costelli, J. and Hecht. M., 1971. The postcranial osteology of the lizard *Shinisaurus:* the appendicular skeleton. *Herpetologica*, 27: 87-98.

Cree, A., and Daugherty, C. 1990. Tuatara sheds its fossil image. *New Scientist* 128, 1739: 30-34.

Crisci, J.V., and Stuessy, T. F. 1980. Determining primitive character states for phylogenetic reconstruction. *Systematic Botany*, 5: 112-135.

Daugherty, C. H., and Cree, A., 1990. Neglected taxonomy and continuing extinctions of tuatara *(Sphenodon)*. *Nature*, 347: 177-179.

Densmore, L.D. and Owen, R.D. 1989. Molecular systematics of the order Crocodilia. *American Zoolology*, 29:831-841.

De Queiroz, K. 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Systematic Zoology*, 34: 280-299.

----, 1987. Phylogenetic systematics of iguanine lizards: A comparative osteological study. *University of California Publicatgions in Zoology*, 118: 12- 203.

Devilliers, C. 1954. Structure et évolution de la colonne vertébrale. Les côtes. Le sternum. pp. 605-709. In, Grasse, P. P. (ed.), *Traité de Zoologie*. Masson et Cie, Paris.

Dollo, L. 1884. Sur les épiphyses des lacertiliens. *Zoologischer Anzeiger*, 160: 80-84.

Duellman, W. E., and Heatwole, H. 1992. pp 126-174. Habitats and adaptations. In, Cogger, H. G. and Zweifel, R. G. (ed.), *The Encyclopedia of Reptiles and Amphisbians*. Part 3. Academic Press, USA.

Edgeworth, F. H. 1935. *The Cranial Muscles of Vertebrates*. Cambridge University Press. 493 pp.

El-Toubi, M. R. 1938. The osteology of the lizard *Scincus scincus*. *Bulletin, Faculty of Science*, 14: 5-38.

----, 1945. Notes on the cranial osteology of *Uromastyx aegyptius*. *Bulletin, Faculty of Science*, 25: 1-10.

----, 1947. Some observations on the osteology of the lizard, *Agama stellio*. *Journal of Morphology*, 81: 135-149.

----, and Khalil, A. 1952. The cranial osteology of Egyptian Geckos. *Bulletin de l'Institut Fouad Ier du Desert*, 11: 84-110.

----, and Khalil A. 1955. The post-cranial osteology of Egyptian geckos. *Bulletin de l'Institut Fouad Ier du Desert*, 5 (1): 99-136.

Essex, R. 1927. Studies in reptilian degeneration. *Proceedings of the Zoological Society of London*, 1927/1928: 879-945.

Estes, R. 1983. The fossil record and early distribution of lizards. pp. 365-398. In, Rhodin, A.G.J. and Miyata, K. (eds.), *Advances in Herpetology and Evolutionary Biology*. Cambridge, Massachusetts: Museum of Comparative Zoology.

Estes, R., de Queiroz, K., and Gauthier, J. A. 1988. Phylogenetic relationships of squamate reptiles. pp. 119-270. In, Estes, R. and Pregill, G. (ed.), *Phylogenetic Relationships of Lizard Families*. Stanford University Press, Stanford, California.

Etheridge, R. 1964. The skeletal morphology and systematic relationships of sceloporine lizards. *Copeia*, 4: 610-631.

----, and de Queiroz, K. 1988. A phylogeny of Iguanidae. pp. 183-367. In, Estes, R. and Pregill, G. (ed.), *Phylogenetic Relationships of Lizard Families*. Stanford University Press, Stanford, California.

Evans, S. E. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society*, 70: 203-264.

----, 1981. The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis. Zoological Journal of the Linnean Society*, 73: 203-64.

----, 1982. The gliding reptiles of the Upper Permian. 2001. *Journal of the Linnean Society of London*, 76 (2): 97 – 123.

---- 1984. The classification of the Lepidosauria. *Zoological Journal of the Linnean Society*, 82: 87-100.

---- 1988. The early history and relationships of the Diapsida. pp. 221-253. In, Benton, M.J. (ed), *The phylogeny and classification of the tetrapods*. Oxford. Oxford University Press.

---- 1991. A new lizard-like reptile (Diapsida: Lepidosauromorpha) from the Middle Jurassic of Oxfordshire. *Zoological Journal of the Linnean Society*, 103: 391-412.

---- 1994. A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Paleontology*, 37: 33-49.

---- 1998. Crown group lizards from the Middle Jurassic of Britain. *Paleontographica*, 250: 123-154.

Evans, S. E., and Barbadillo, L. J. 1997. Early Cretaceous lizards from Las Hoyas, Spain. *Zoological Journal of the Linnean Society*, 119: 23-49.

----, and Chure, D. C. 1998. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology*, 18: 99-114.

Evans, S. E., Prasad, G.V.R., and Manhas, R. S. 2000. Jurassic vertebrates from India: new microvertebrates from the Kota formation of Andhra Pradesh. *Journal of Vertebrate Paleontology*, 20: 40A.

Farris, J. S. 1982. Outgroups and parsimony. *Systematic Zoology*, 31: 328-334.

Filan, S. L. 1990. Myology of the head and neck. *Australian Journal of Zoology*, 38: 617- 34.

Forey, P. L., Humphries, C. J., Kitching, I. L., Scotland, R. W., Siebert, D. J., and Williams, D. M. 1992. *Cladistics (A Practical Course in Systematics)*. The Systematics Association Publication No. 10, Clarendon Press, Oxford. I89 pp.

Fraser, N. C. 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London*, 321 (1204): 125-178.

Fraser, N. C., and Benton, M. J. 1989. The Triassic reptiles *Brachyrhinodon* and *Polysphenodon* and the relationships of the sphenodontids. *Zoological Journal of the Linnean Society*, 96: 413-445.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. *Journal of Morphology*, 111: 287-319.

----, 1986. The origin of amphikinesis in lizards. A problem in functional morphology and the evolution of adaptive systems. *Evolution Biology*, 20: 419-461.

Frey, E., Riess, J., and Tarsitano, S. F. 1989. The axial tail musculature of recent crocodiles and its phyletic implications. *American Zoologist*, 29: 857-862.

Frost, D. R. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). *American Museum Novitates*, 3033: 1-68.

----, and Etheridge, R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptila: Squamata). Miscellaneous Publications, The University of Kansas, *Museum of Natural History*, 81: 1-65.

Ganguly, D. N., and Mitra, B. 1958. On the structure and the development of the vertebral column in the House-Gecko, *Hemidactylus flaviviridis. Anatomische Anzeige*, 105(1/5): 4-25.

Gans, C. 1960. Studies on amphisbaenids (Amphisbaenia, Reptilia). A taxonomic revision of the Trogonophinae and a functional interpretation of the amphisbaenid adaptive pattern. *Bulletin of the American Museum of Natural History*, 119: 129-204.

----, 1962. Terrestrial locomotion without limbs. *American Zoologist*, 2: 167-182.

----, 1966a. Some limitations and approaches to problems in functional anatomy. *Folia Biotheoretica*, 6: 41-50.

----, 1966b. The functional basis of the retroarticular process in some fossil reptiles. *Journal of Zoology*, 150: 273-277.

----, 1967. The Chamaeleon. *Natural History*, 76: 52-59.

----, 1969a. Amphisbaenians – reptiles specialized for a burrowing existence. *Endeavour*, 28: 146-151.

----, 1969b. Functional components versus mechanical units in descriptive morphology. *Journal of Morphology*, 128: 365-368.

----, 1973a. Uropeltid snakes – survivors in a changing world. *Endeavour*, 32: 6-65.

----, 1973b. Locomotion and burrowing in limbless vertebrates. *Nature*, 242: 414-415.

----, 1978. The characteristics and affinities of the Amphisbaenia. *Transactions of the Zoological Society of London*, 34:347-416.

----, 1980. *Biomechanics*. approach to vertebrate biology. The University of Michigan Press. Ann Arbor. 261 pp.

----, 1985. Limbless locomotion – a current overview. *Fortschritte der zoologie*, 30: 13-22.

----, 1992a. Why develop a neck? pp. 17-21. In, Berthoz, A., Vidal, P. P. & Graf, W. (ed), *The head neck sensory motor system.* Oxford University Press, New York.

----. 1992b. Amphisbaenians. pp. 212-217. In, Cogger, H.G. and Zweifel, R.G (ed.), *The Encyclopedia of Reptiles and Amphisbians*, Part 3. Academic Press, USA.

----, and Fusari, M. 1994. Locomotor analysis of surface propulsion by three species of reduced limbed fossorial lizards (*Lerista*: Scincidae) from Western Australia. *Journal of Morphology,* 222: 309 – 326.

Gao K. and Norell, M. A. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of the anguimorphan lizards. *American Museum Novitates* 3230: 1-51.

Gardner, J. D. and Cifelli, R. 1999. A primitive snake from the Cretaceous of Utah. *Special paper in Palaeontology,* 60: 87-100.

Gasc, J. P. 1967. Introduction a l'etude de la musculature axiale des squamates serpentiforms. *Mémoires du Muséum Nationale d'histoire Naturelle,* Paris, 48A: 69-125.

----, 1981. Axial musculature. pp. 355-435. In, Gans, G. and Parsons, T. S. (eds.), *Biology of the Reptilia.* Academic Press, London and New York.

----, and Gans, C. 1990. Tests on the locomotion of the elongate and limbless reptile *Anguis fragilis. Copeia* 1990: 1055 – 1067.

Gaupp, E. 1900. Das Chondrocranium von *Lacerta agilis.* Ein Beitrag zum verständnis des Amniotenschädels. *Anatomische Hefte.* XV: 435-595.

Gauthier, J. 1982. Fossil Xenosauridae and Anguidae from the Lower Eocene Wasatch Formation, southcentral Wyoming, and a revision of the Anguioidae. *Contributions to Geology.* University of Wyoming, 21: 7-54.

----. 1984. *A cladistic analysis of the higher systemic categories of the Diapsida.* Ph.D. thesis, Department of Paleontology, University of California, Berkeley. USA. 572 pp.

----, Estes, R., and de Queiroz, K. 1988. A phylogenetic analysis of the Lepidosauromorpha. pp. 15-98. In, Estes, R. and Pregill, G. (ed.), *Phylogenetic Relationships of the Lizard Families.* Stanford University Press, Stanford. California.

George, J. C. 1948. The muscular system of *Uromastyx hardwickii*. *Journal of theUniversity of Bombay*, 17b (3): 1-23.

----, and Shah, R. V. 1954. The myology of the head and neck of the common Indian pond turtle, *Lissemys punctata granosa*. *Journal of Animal Morphology and Physiology*, 1: 1-12.

----, and ----. 1955. The myology of the head and neck of the Indian tortoise, *Testudo elegans*. *Journal of Animal Morphology and Physiology*, 2: 1-13.

Gilmore, C. W. 1928. *Fossil lizards of North America*. Memoirs of the National Academy of Sciences, volume 22 / number. 3. Washington, 201 pp.

Goodrich, E. S. 1930. *Studies on the structure and development of vertebrates*. Macmillan. London. 837 pp.

Gould, S. 1966. Allometry and size in ontogeny and phylogeny. *Biological reviews, Cambridge Philosophical Society*, 41: 587 – 640.

Gow, C. E. 1975. The morphology and relationships of *Youngina capensis* and *Prolacerta broomi* Parrington. *Palaeontologia africana*, 18: 89-131.

Gray, J. 1946. The mechanism of locomotion in snakes. *Journal of Expermental Biology*, 23: 101-120.

----, and Lissmann, H. W. 1950. The kinetics of locomotion of the grass-snake. *Journal of Expermental Biology*, 26: 354-367.

Greer, A. E. 1970. A subfamilial classification of scincid lizards. *Bulletin of the Museum of Comparative Zoology*. 139: 151-184.

----, 1985. The relationships of the lizard genera *Anelytropsis* and *Dibamus*. *Journal of Herpetology* 19: 116-156.

Grismer, L. L. 1988. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos. pp. 369-469. In, Estes, R. and Pregill, G. (ed.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press, Stanford, Clifornia.

Guibé, J. 1970. Anatomie des Reptiles. la musculature. pp. 144-180. In, Grasse, P. P. (ed.), *Traité de Zoologie*. Volume 14/ number 2. Masson, Paris.

Günther, A. 1867. Contribution to the anatomy of *Hatteria* (*Rhynchocephalus* Owen). *Philosophical Transactions of the Royal Society*, London, 167: 595-629.

Haas, G. 1973. Muscles of the jaws and associated structures – Rhynchocephalia and Squamata. pp. 285-420. In, Gans C. (ed.), *Biology of the Reptila*. Volume 4, Academic Press. London and New York.

----, 1980. *Pachyrhachis problematicus*, snake-like reptile from the Lower Cenomanian: ventral view of the skull. *Bulletin de la Museum Nationale d'Histoire Naturelle*, Paris, 4 (2): 87-104.

Hallerman, J. 1998. The ethmoidal region of *Dibamus taylori* (Squamata: Dibamidae), with a phylogenetic hypothesis on dibamid relationships within Squamata. *Zoological Journal of the Linnean Society*, 122: 385-426.

----, and Böhme, W. 2000. A review of the genus *Pseudocalotes* (Squamata: Agamidae), with description of a new species from West Malaysia. *Amphibia-Reptilia*, 21: 193-210.

Halliday, T., and Adler, K. 1986. *The Encyclopaedia of Reptiles and Amphibians*. Equinox Ltd., Oxford. 143 pp.

Haskell, B., Day, M. and Tetz, J. 1986. Computer-aided modeling in the assessment of the biomechanical determinants of diverse skeletal patterns. *American Journal of Orthodontics*, 89: 363-382.

Hennig, W. 1965. Phylogenetic systematics. *Annual review of the Entomology*, 10: 97-116.

----, 1966. *Phylogenetic systematics*. University of Illinois Press, Urbana. 263 pp.

Herrel, A., Aerts, P., De Vree, F. 1998. Ecomorphology of the lizard feeding apparatus: a modelling approach. *Netherland Journal of Zoology* 48(1): 1-25.

Herrel, A., and De Vree F. 1999. The cervical musculature in helodermatid lizards. *Belgian Journal of Zoology*. 129: 175-185.

Herring, S.W. 1993. Epigenetic and functional influences on skull growth. pp. 153-206. In, Hanken, J. and Hall, B. K. (ed.), *The skull*. Volume (1), Chicago, University of Chicago Press.

Hoffstetter, R. and Gayrard, Y. 1964. Observations sur l'ostéologie et la classification des Acrochordidae (Serpentes). *Bulletin of the Museum of the Natural History*, Paris, 36: 677-696.

Hoffstetter, R. and Gasc, J. P. 1969. Vertebrae and ribs of modern reptiles. pp. 201-310. In, Gans, C. Bellairs, C. and Parsons, T. (eds.), *Biology of the Reptilia*. Volume (1), Published by Academic Press.

Holder, L. A. 1960. The comparative morphology on the axial skeleton in the Australian Gekkonidae. *Journal of Linnean Society, London*. 44: 300-335.

Howell, A. B., 1936. Morphogenesis of the shoulder architecture. *Quarterly Review of Biology*, Baltimore, 112: 183-208.

Howes, G. B., and Swinnerton, H. H. 1901. On the development of the skeleton of the Tuatara, *Sphenodon punctatus*, with remarks on the egg, on the hatching, and on the hatched young. *Transactions of the Zoological Society of London*, 16: 1-74.

Hyman, L. H. 1942. *Comparative vertebrate anatomy*, second edition, University of Chicago Press. 544 pp.

Iordansky, N. N. 1964. The jaw muscles of the crocodiles and some related structures of the crocodilian skull. *Anatomischer Anzeiger*, 115: 256-280.

----, 1973. The skull of the Crocodilia. pp. 201-262. In, Gans, C. and Parsons, T. (ed.), *Biology of the Reptilia*, volume (4), Academic Press, London.

Islam, A. 1956. The postcranial skeleton of *Uromastyx hardwickii*. *Biologia*, Lahore, 2: 231-246.

Magnusson, W. E. 1992. Body temperatures of field active Amazonian Savanna Lizards. *Journal of Herpetology*, 27: 53-58.

Mahendra, B. C., 1936. Contributions to the osteology of the Ophidia. The endoskeleton of the so called "Blind Snake", *Typhlops braminus*. *Proceedings of the Natural Academy of Sciences*, India, 3: 128-142.

----, 1949. The skull of the Indian house-gecko, *Hemidactylus flaviviridis*. *Proceedings of the Zoological Society*, (Calcutta), 2: 29-42.

----, 1950. The osteology of the Indian house-gecko, *Hemidactylus flaviviridis*. *Proceedings of the Zoological Society*. (Bengal), 3 (1): 49-64.

Maslin, P. P. 1952. Morphological criteria of phylogenetic relationships. *Systematic Zoology*, 1: 49-70.

McDowell, S. B 1972. The evolution of the tongue of snakes, and its bearing on snake origins. pp. 191-273. In, Dobzhansky, M., Hecht, K. and Steere, W. C. (ed.), *Evolutionary Biology*. Volume (6). Appleton-Century-Crofts, New York.

McDowell, S. B. Jr., and Bogert, C. M. 1954. The systematic position of *Lanthanotus* and the affinities of the anguinomorphan lizards. *Bulletin of the American Museum of Natural History*, 105(1): 1-142.

Mertens, R. 1960. *The World of Amphibians and Reptiles*. George G. Harrap & Co. Ltd London. 207 pp.

Mivart, G. St. 1870. On the myology of *Chamaeleon parsonii*. *Proceedings of the Zoological Society*, London, 38: 850-890.

Moffat, L. A., 1973. Mechanics of intercentral joints in the Gekkota (Reptilia: Lacertilia). *Journal of Anatomy*, 116: 476.

Moody, S. M. 1980. *Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia; Lacertilia)*. Ph.D. thesis, University of Michigan. 390 pp.

Mook, C. C. 1921. The dermo-supraoccipital bone in the Crocodilia. *Bulletin of the American Museum of Natural History*, 44(9): 101 – 103.

----, 1934. Evolution and classification of Crocodilia. *Journal of Geology*, 42(3): 295-304.

Moro, S., and Abdala, V. 1998. Cranial myology of some species of *Liolaemus* and *Phymaturus* (Squamata: Tropiduridae: Liolaeminae). *Amphibia-Reptilia*, 19: 171-192.

Mosauer, W. 1935. The myology of the trunk region of snakes and its significance for ophidian taxonomy and phylogeny. University of California, *Biological Science*, 1(6): 81-120.

Murakami, G. 1988. Nerve supply of the ventral trunk musculature of the brown Caiman (*Caiman crocodilus fuscus*: Alligatoridae, Crocodilia), and its morphological consideration. *Acta Anatomica Nippomica*, 63: 22-38.

----, Akita, K., and Sato, T. 1991. Arrangement and innervation of the iliocostalis and longissimus muscles of the brown Caiman (*Caiman crocodilus fuscus*: Alligatoridae, Crocodilia). *The American Journal of Anatomy*, 192: 241-256.

Necas, P. 1999. "Chameleons-Nature's hidden jewels". 1st edition, Frankfurt. 348 pp.

Netter, F. 1998. *Atlas of Human Anatomy*. Icon Learning Systems. Second edition. New Jersey. 525 pp.

Newman, D. G. 1987. Burrow use and population densities of tuatara (*Sphenodon punctatus*) and how they are influenced by *Pachyptila turtur* on Stephens Island, New Zealand. *Herpetologica*, 43: 336-344.

Nishi, S. 1916. Zur vergleichenden Anatomie der eigentlichen (genuinen) Rückenmuskelen. *Morphologisches Jahrbuch*, 50: 219-247.

Noble, G. K. 1921. The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera with the description of a new genus. *American Museum Novitates*. 4: 1-16.

Nopcsa, F. 1928. The genera of reptiles. *Paleobiologica*, 1: 163 – 88.

----, 1930. Ueber prozöle und opisthozöle Wirbel. *Anatomischer Anzeiger*, 69 (1/3): 19-25.

Oelrich, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *Miscellaneous Publications, Museum of Zoology*, University of Michigan, 94: 1-122.

Osborn, H.F. 1900. Intercentra and hypapophyses in the cervical region of mosasaurs, lizards and *Sphenodon*. *American Naturalist*, 34: 1-7.

----, 1903. The reptilian subclassess Diapsida and Synapsida and the early history of the Diaptosauria. *Memoirs of the American Museum of Natural History*, 1: 449-508.

Owen, R., 1866. *On the Anatomy of Vertebrates*. Volume (1), Fishes and reptiles. Longmans, Green and Co., London.

Paranjape, S.Y. 1974. *The Anatomy of the Garden Lizard. Zoological Monograph*. University of Poona. 173 pp.

Parker, H. W. 1977. *Snakes: a natural history*. Second edition. British Museum (Natural History). Cornell University Press. Ithaca and London. 106 pp.

Parker, W. K. 1868. *A monograph on the structure and development of the shoulder – girdle in the Vertebrata*. London Royal Society. 237 pp.

Penning, L. 1968. *Functional pathology of the cervical spine*. Excerpta Media Foundation, Amsterdam. 196 pp.

Peters, G. 1982. Phylogenetische Probleme des Lepidosauria. *Vertebrata Hungarica*, 21: 209 – 213.

Peterson, J. A. 1973. *Adaptation for Arboreal Locomotion in the Shoulder Region of Lizards*. Ph.D. Thesis: University of Chicago. 111 pp.

Pleguezuelos, J., Poveda, J., Monterrubia, R. and Ontiveros, O. 1999. Feeding habits of common chamaeleon, *Chamaeleo chamaeleon* in the Southeast Iberian Peninsula. *Israel Journal of Zoology*, 45: 267-276.

Pregill, G. K., Gauthier, J. A., and Greene, H. W. 1986. The evolution of helodermatid squamates, with a description of a new taxon and an

overview of Varanoidea. *Transactions of the San Diego Society of Natural History*, 21: 167-202.

Presch, W. 1969. Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae). *Copeia*, 1969: 250-275.

----, 1988. Phylogenetic relationships within the Scincomorpha. pp. 471-492. In, Estes, R. and Pregill, G. (ed.). *Phylogenetic relationships of the lizard families*. Stanford University Press, California.

Pritchard, P. C. H. 1984. Piscivory in turtles and evolution of the long-necked Chelidae. *Symposia of the Zoological Society of London*, 52: 87 –110.

Ramaswami, L.S. 1952. The fully formed chondrocranium of *Mabuya* with an account of the adult osteocranium. *Acta Zoologica Stockholm*, 33: 209-275.

Reese, A. M. 1923. The osteology of the tegu, *Tupinambis nigropunctatus*. *Journal of Morphology*, 38: 1-18.

Reeve, W. L. 1952. Taxonomy and distribution of the horned lizard *Phrynosoma*. Kansas University. *Scientific Bulletin*, 34: 817-960.

Reisz, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. *Special Publications of the Museum of National History*, University of Kansas, 7: 1-74.

Rensch, B. 1959. *Evolution above the species level*. First edition, New York. 419 pp.

Reynoso, V. H. 1998. *Huehuecuetzpalli mixtecus*: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. *Philosophical Transactions of the Royal Society. Biological Sciences*, 353: 477-500.

Richmond, F. J. R., and Armstong, J. B. 1988. Fiber architecture and histochemistry in the cat neck muscle, biventer cervicis. *Journal of Neurophysiology*, 60: 46-59.

Rieppel, O. 1976. On the presence and function of post-cloacal bones in the Lacertilia. *Monitore Zoologica Italiano*, 10: 7-13.

----, 1979. A cladistic classification of primitive snakes based on skull structure. *Systematic and Evolutionsforschung*, 17: 140 – 50.

----, 1980. The phylogeny of anguimorph Lizards. *Denkschriflen der Schweizerischen Naturforschenden Gesellschajt*, 94: 1-86.

----, 1981. The skull and jaw adductor musculature in chamaeleons. *Revue suisse de zoologie*, 88: 433-445.

----, 1982. The phylogenetic relationships of the genus *Acontophiops sternfeld* (Sauria: Scincidae), with a note on mosaic evolution. *Annals of the Transvaal Museum*, 33: 241 – 57.

----, 1984. The cranial morphology of the fossorial lizard genus *Dibamus* with a consideration of its phylogenetic relationships. *Journal of Zoology*, 204: 289-327.

----, 1987. The phylogenetic relationships within the Chamaeleonidae, with comments on some aspects of cladistic analysis. *Zoological Journal of the Linnean Society*, 89: 41-62.

----, 1988. The classification of the Squamata. pp. 261-293. In, Benton, M. J. (ed). *The phylogeny and classification of the tetrapods*. Oxford University press, Oxford.

----, 1993. Patterns of diversity in the reptilian skull. pp. 391-437. In, Hanken, J. and Hall, B.K. (ed.), *The skull*. Volume (2), University of Chicago Press, Chicago.

----, and Crumly, C. 1997. Paedomorphosis and skull structure in Malagasy chamaeleons (Reptilia: Chamaeleoninae). *Journal of Zoology*, 243: 351-380.

----, and Zaher, H. 2000. The braincases of mosasaurs and *Varanus*, and the relationships of snakes. *Zoological Journal of the Linnean Society*, 129: 489-514.

Rinker, G. C. 1954. The comparative myology of the mammalian genera *Sigmodon, Oryzomis, Neotoma* (Creetinae), with remarks on their intergeneric relationships. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 83 : 1-13.

Robinson, P. L. 1962. Gliding lizards from the Upper Keuper of Great Britain. *Proceedings of the Geological Society of London*, 1601: 137-146.

Rogner, M. 1997. *Lizards*. Volume 1. Krieger Publishing Company Malabar, Florida. 317 pp.

Romer, A. S. 1956. *Osteology of the Reptiles*. University of Chicago Press, Chicago. 772 pp.

Ruckes, H. 1929. Studies in chelonian osteology. The morphological relationships between the girdles, ribs and carapace. *Annals of the New York, Academy of Sciences*, 31: 81-119.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs. *Peabody Museum of Natural History, Yale, Bulletin*, 23: 1-241.

Saint Girons, H. 1970. The pituitary gland. pp. 135-99. In, Gans, C. and Parsons, T. S. (ed.), *Biology of the Reptilia*. Volume (3), Academic Press, London.

Savage, J. M. 1963. Studies on the lizard family Xantusiidae. The genera. *Contributions in Science, Natural History Museum of Los Angeles County*, 71: 1-38.

Schwenk, K. 1988. Comparative morphology of the lepidosaur tongue and its relevance to squamate phylogeny. pp 569-598. In, Estes, R. and Pregill, G. (ed.), *Phylogenetic Relationships of the Lizard Families*. Stanford University Press Stanford, California.

----, 2000. *Feeding*: Form, Function, and Evolution in Tetrapod vertebrates. Ist edition, Academic Press, London. 537 pp.

Seidel., R. 1978. *The somatic musculature of the cervical and occipital regions of Alligator mississipiensis*. Unpublished PhD. Thesis, City University of New-York. New York. 1079 pp.

Shah, R.V. 1963. The neck musculature of a cryptodire (*Deirochelys*) and a pleurodire (*Chelodina*) compared. *Bulletin of the Museum of Comparative Zoology*, 129: 343-368.

Shine, R. Snakes. 1992. pp. 126-174. In, Cogger, H.G. and Zweifel R.G (ed.), *The Encyclopedia of Reptiles and Amphisbians*, part (3). Academic Press, USA.

Siebenrock, F., 1893. Das Skelet von *Brookesia superciliaris. Sitzungsberichte der mathematisch – naturwissenschaftlichen classe der Kaiserlichen Akademie der Wissenschaften*, 102(1): 71-118.

Singh, L. A. K., Acharjyool, N., and Bustard, H.R. 1984. Observations of the reproductive biology of the Indian Chameleon. *Chamaeleo zeylanicus. Journal of the Bombay Natural History Society*, 81(1): 86-92.

Skinner, J. 1959. Ontogeny of the breast-shoulder apparatus of the South African lacertilian, *Microsaura pumila pumila. Annales University of Stellenbosch*, 35: 5-66.

Smith, L.A. 1976. The reptiles of Barrow Islands. Western Australia. *Nature*, 13(6): 125-136.

Smith, K. 1980. Mechanical significance of streptostyly in lizards. *Nature*, 283:778-779.

----, 1982. An electromyographic study of the function of the jaw adducting muscles in *Varanus exanthematicus* (Varanidae). *Journal of Morphology*, 173 : 137-158.

Sood, M. S. 1948. The anatomy of the vertebral column in serpents. *Proceedings of the Indian National Science Academy*, 28: 1-26.

Steel, R. 1973. Crocodylia. pp. 1-116. In, Kuhn, O. (ed.), *Handbuch der Palaoherpetologie*. Fischer Verlag, Stuttgart.

Stevens, P. F. 1980. Evolutionary polarity of character states. *Annual review of Ecology and Systematics*, 11: 333-358.

Tarsitano, S.F., Frey, E., and Riess, J. 1989. The evolution of the Crocodilia: A conflict between morphological and biochemical data. *American Zoologist*, 29: 843-856.

Tchernov, E., Rieppel, O., Zaher, H., Polcyn, M. J., and Jacobs, L. L., 2000. A fossil snake with limbs. *Science*, 287: 2010-2012.

Tilak. R. 1964. The osteology of *Uromastyx hardwickii. Zoologischer Anzeiger*, 173: 403-426.

Underwood, G. L., 1954. On the classification and evolution of geckos. *Proceedings of the Zoological Society of London*, 124: 469-492.

----, 1957. On the lizards of the family Pygopodidae: A contribution to the morphology and phylogeny of the Squamata. *Journal of Morphology*, 100(2): 207-268.

Wahba, M. T., Khalil, A., and Shawki, N. A. 1992a. The post-cranial myology of *Agama mutabilis*, Family: Agamidae. 1-Axial muscles (cervical region). *Assuit Veternary Medical Journal*, 53: 81-91.

----, ----, and ----, 1992b. The post-cranial myology of *Chamaeleo vulgaris*, Family: Chamaeleontidae. 1- Axial muscles (cervical region). *Assiut Veternary Medical Journal*, 53: 68-80.

----,----, and ----, 1992c. Studies on the post-cranial myology of *Tarentola annularis*, Family: Geckonidae. L- Axial muscles (cervial region). *Assuit Veternary Medical Journal*, 53: 55-67.

Walker, A.D. 1970. A revision of the Jurassic reptile *Hallopus victor*, Marsh with remarks on the classification of crocodiles. *Philosophical Transactions of the Royal Society, Biological Sciences*, 257: 323-372.

Warfel, J.H. 1993. *The Head, Neck, and Trunk*, Sixth edition. Lea and Febiger. Philadelphia and London. 143 pp.

Watrous, L. E., and Wheeler, Q. D. 1981. The outgroup comparison method of character analysis. *Systematic Zoology*, 30: 1-11.

Webb, J.E., Wallwork J.A., and Elgood J.H. 1978. *Guide to Living Reptiles*. The Macmillan Press Ltd. London. 171 pp.

Wermuth, H. 1953. Systematic der rezenten Krokodile. *Mitteilungen der Zoologischen Museum of Berlin*, 29: 375-514.

Whetstone, K. N., and Whybrow, P. J. 1983. A 'cursorial' crocodilian from the Triassic of Lesotho (Basutoland) Southern Africa. *Occasional Papers of the Museum of Natural History of Kansas*, 106: 1-37.

Whiteside, D. I. 1986. The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonensis*, and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London*, 312(1156): 379-430.

Williams, E. E. 1950. Variation and selection in the cervical central articulations of living turtles. *Bulletin of the American Museum of Natural History*, 94(9): 505-562.

Wu, Xiao-chun., Brinkman, D.B., Russell, A. P., Zhi-min dong, P. J., Currie, Lian-hai Hou., and Gui-hai, Cui. 1993. Oldest known amphisbaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature*, 366: 57-59.

----, ----, ----. 1996. *Sineoamphisbaena hexatabularis*, an amphisbaenian (Diapsida, Squamata) from the Upper Cretaceous redbeds at Bayan Mandahu (Inner Mongolia, People's Republic of China), and comments on the phylogenetic relationships of the Amphisbaenia. *Canadian Journal of Earth Sciences*, 33: 541-577.

Young, J. Z. 1981. *The Life of Vertebrates.* Clarendon Press, Oxford. 767 pp.

Zaaf, A., Herrel, A., Aerts, P., and DeVree, F. 1999. Morphology and morphometrics of the appendicular musculature in geckos with different locomotor habits (Lepidosauria). *Zoomorphology*, 119: 9-22.

Zangerl, R, 1944. Contributions to the osteology of the skull of the Amphisbaenidae. *American Midland Naturalist*, 31: 417-454.

----, 1945. Contributions to the osteology of the postcranial skeleton of the Amphisbaenidae. *American Midlland Naturalist*, 33(3): 764-780.

Zug, G. R. 1993. *Herpetology, an Introductory Biology of Amphibians and Reptiles.* Academic Press. San Diego, California. 527 pp.

Zusi, R. L. 1985. Muscles of the neck, trunk and tail in the noisy Scrub-Bird, *Atrichornis clamosus* and superb Lyrebird, *Menura novaehollandiae* (Passeriformes; Atrichornithidae and Menuridae). *Records of the Australian Museum*, 137: 229 – 271.

Zweers, G. 1982. Pecking of the pigeon (*Columa livia*). *Behaviour*, 81: 174-230.

Zweers, G., Bout, R and Heidweiller, J. 1994. pp. 201-221, Motor organization of the avian head-neck system. In, Davies, M. N. O and Green P. R. (Ed). *Perception and motor control in birds.* Springer, Berlin.

VI - APPENDIX

LIST OF ABBREVIATIONS FOR MUSCLES

ABBREVIATIONS	MUSCLES
A-oop	Atlas to oto-occipital
A-Cr3	Atlas transverse process to third cervical rib
A-popp	Atlas transverse process to paroccipital process
Ax-sop	Axis to supraoccipital
Ax-Ana	Axis to atlas neural arch
Bop-Cl	Basioccipital to clavicle
Bop-Q	Basioccipital to quadrate
C&TcTd	Cervical and trunk central tendon
Cm	Cervicomandibularis
Cl-Bop	Clavicle to basioccipital
Ct-Tvp	Centra to transverse process
Cstc	Constrictor colli
Cld	Clavicle dorsalis
Cl/Icl-Sq	Clavicle/interclavicle to squamosal
Cr (1-4)-Ic&c	Cervical rib (1-4) to intercentra and centra
Cr-Ssp	Cervical rib to suprascapula
Cr1-Ssp	Cervical rib 1 to suprascapula
Cr2-Ssp	Cervical rib 2 to suprascapula
Cr3-Ssp	Cervical rib 3 to suprascapula
Cr(1-5)-Ssp	Cervical rib 1 to 5 to suprascapula
Cr(1-2)-Ssp/Sd	Cervical ribs 1 and 2 to suprascapula and scapulocoracoid
C2-3 Tvp	Cervical 2 to cervical 3 transverse process
Drm	Depressor mandibulae
Drmi	Depressor mandibulae internus
Drme	Depressor mandibulae externus
(D)Cr-Ssp/Sd	Deep cervical ribs to suprascapula and scapulocoracoid
(D)Cr2-Ssp	Deep cervical rib 2 to suprascapula
(D)Cr3-Ssp	Deep cervical rib 3 to suprascapula
(D)Ic1-Oop	Deep intercentra 1 to oto-occipital
(D)Ic1-Bop/Oop	Deep intercentral to basioccipital and oto-occipital
Dr1-Ssp/Sd	Dorsal rib 1 to scapulacoracoid/suprascapula
Dr1-Ssp	Dorsal rib 1 to suprascapula
Dr3-Sd/Ssp	Dorsal rib 3 to scapulocoracoid and suprascapula
Dr(1-4)-Ssp	Dorsal ribs 1 to 4 to suprascapula
Ecm	Episternocleidomastoid
Hyp-Ssp	Hypapophyses to suprascapula
Hyp1-Bop	Hypapophysis 1 to basioccipital
Hyp(4-7)-Sd&Cv	Hypapophyses 4 to 7 to scapulacoracoid and clavicle
Hyp (2-6)- Bop/Oop	Hypapophyses 2 to 6 to basioccipital and oto-occipital
Hyp-r	Hypapophyses to rib distal end
Hyp-pap/rl	Hypapophyses to parapophysial processes/rib ligaments
Ic-rl	Intercentra to rib ligaments

Ic1m	Intercentrum muscle
Ic1-Ssp	Intercentrum 1 to suprascapula
Ic-Ssp & r	Intercentra to suprascapula and rib
Ic-rp	Intercentra to rib processes (short muscles)
Ic1-Bop	Intercentrum 1 to basioccipital
Ic-Bop/Oop	Intercentra to basioccipital and oto-occipital
Ic1-Bop/Oop	Intercentrum 1 to basioccipital and oto-occipital
Ic2-Bop/Oop	Intercentrum 2 to basioccipital and oto-occipital
Ic(1-4)-Bop/Oop	Intercentra 1 to 4 to basioccipital and oto-occipital
Ic(2-5)-Bop/Oop	Intercentra 2 to 5 to basioccipital and oto-occipital
Ic(2-3)-Oop	Intercentra 2 and 3 to oto-oto-occipital
Ic-r	Intercentra to adjacent ribs
Ic1-Ssp	Intercentrum 1 to suprascapula
Ic (2-5)-Cr3	Intercentra 2 to 5 to cervical rib 3
Ic (2-4)-Cr(4-5)	Intercentra (2-4) to cervical rib (4-5)
Ic2-Oop	Intercentrum 2 to oto-occipital
Ic3-Oop	Intercentrum 3 to oto-occipital
Ic3-Bop	Intercentrum 3 to basioccipital
Ic4-Oop	Intercentrum 4 to oto-occipital
Ic3-Tvp	Intercentrum 3 to transverse process
Ic (2-4)- Oop	Intercentra 2 to 4 to oto-occipital
Isp	Interspinalis
Ina	Interneural arch
Izyp	Interzygapophyses
Icm	Iliocostalis major
Icc	Iliocostalis cervicus
Iccds	Iliocostalis cervicus dorsalis
Iccv	Iliocostalis cervcius ventralis
Lscp1	Longissimus capitis 1
Lscp1l	Longissimus capitis 1 lateralis
Lscp1m	Longissimus capitis 1 medialis
Lscp2	Longissimus capitis 2
Lscp3	Longissimus capitis 3
Lscp4	Longissimus capitis 4
Lscpm	Longissimus capitis minor
Lsc	Longissimus cervicus
Lsds	Longissimus dorsi
Lsca	Longissimus cervicus anterior
Lscps	Longissimus cervicus posterior
Lci	Longus colli
Lcic	Longus colli centralis
Lcil	Longus colli lateralis
Lc	Longus cervicus
Lcs	Longus cervicus superficialis
Lct	Longus cervicus intermediate
Lcd	Longus cervicus deep
Lcl	Longus cervicus lateralis
Lcm	Longus cervicus medialis
Lci-Icm	Longus colli to iliocostalis major
Lspv	Levator scapula ventralis
Lspd	Levator scapula dorsalis

Ltd	Latissimus dorsi
Mf-Ssp	Muscle fascia to suprascapula
Ocp	Obliquus capitis
Ocpi	Obliquus capitis internus
Ocpe	Obliquus capitis externus
Pl-Q	Parietal to quadrate
Ps	Pectoralis
(Ps)Icm-Sk	Posterior intercentral muscles to skull
(Ps)Ic-Bop	Posterior intercentra to basioccipital
(Ps)Ic-Oop	Posterior intercentra to oto-occipital
(Ps)Hyp-Bop & Oop	Posterior hypapophyses to basioccipital and oto-occipital
Qm	Quadrate (intrinsic) muscle
Rcp	Rectus capitis
Rcpe	Rectus capitis externus
Rcpi	Rectus capitis internus
R-Ssp	Ribs to suprascapula
Sp/Sspcx	Spinalis/semispinalis complex
Sp/Sspc	Spinalis/semispinalis cervicus
Spcp	Spinalis capitis
Spc	Spinalis cervicus
Sspc	Semispinalis cervicus
Sc	Splenius cervicus
Scp	Splenius capitis
Scpi	Splenius capitis internus
Scpe	Splenius capitis externus
Sicr	Sub-iliocostalis rib slips
(Sr)r-Ssp	Superficial ribs to suprascapula
(Sr)Ic1-Bop	Superficial intercentrum 1 to basioccipital
Scpds	Scapula dorsalis
Ssp-mf	Suprascapula to muscle fascia
Tp	Trapezius
Ucp.m	Uncinate process muscle slips
Vp-r	Ventral processes to ribs

LIST OF ABBREVIATIONS FOR BONES

ABBREVIATIONS	BONES
At	Articular
A	Atlas
Ax	Axis
Axct	Axis crest
Ap	Apices
Apx	Apex
Ala	Atlantal arch
Bop	Basioccipital
Bt	Basal tubera
Bct	Basal crest
Br	Bicipital rib

Q	Quadrate
Qj	Quadrojugal
Rp	Retroarticular process
R	Rib
Rl	Rib ligament
S	Spine
Sh	Shaft
Sk	Skull
Sq	Squamosal
St	Supratemporal
Sop	Supraoccipital
Sn	Sternum
Snr	Sternal rib
Sp	Scapula
Ssp	Suprascapula
Sa	Surangular
Sd	Scapulocoracoid
T	Trunk
Tvp	Transverse process
Ucp	Uncinate process
V	Vertebrae
Vp	Ventral process
Vc	Vertebral column
Zy	Zygapophyses
Zm	Zygantrum
Za	Zygantra
Zn	Zygosphene

LIST OF ABBREVIATIONS FOR OTHER STRUCTURES

ABBREVIATIONS	STRUCTURES
& or /	and
-	to
(D)	deep
(Sr)	superficial
e	externus
i	internus
1st	first
2nd	second
3rd	third
4th	fourth
5th	fifth
Mf	muscle fascia
Td	Tendon